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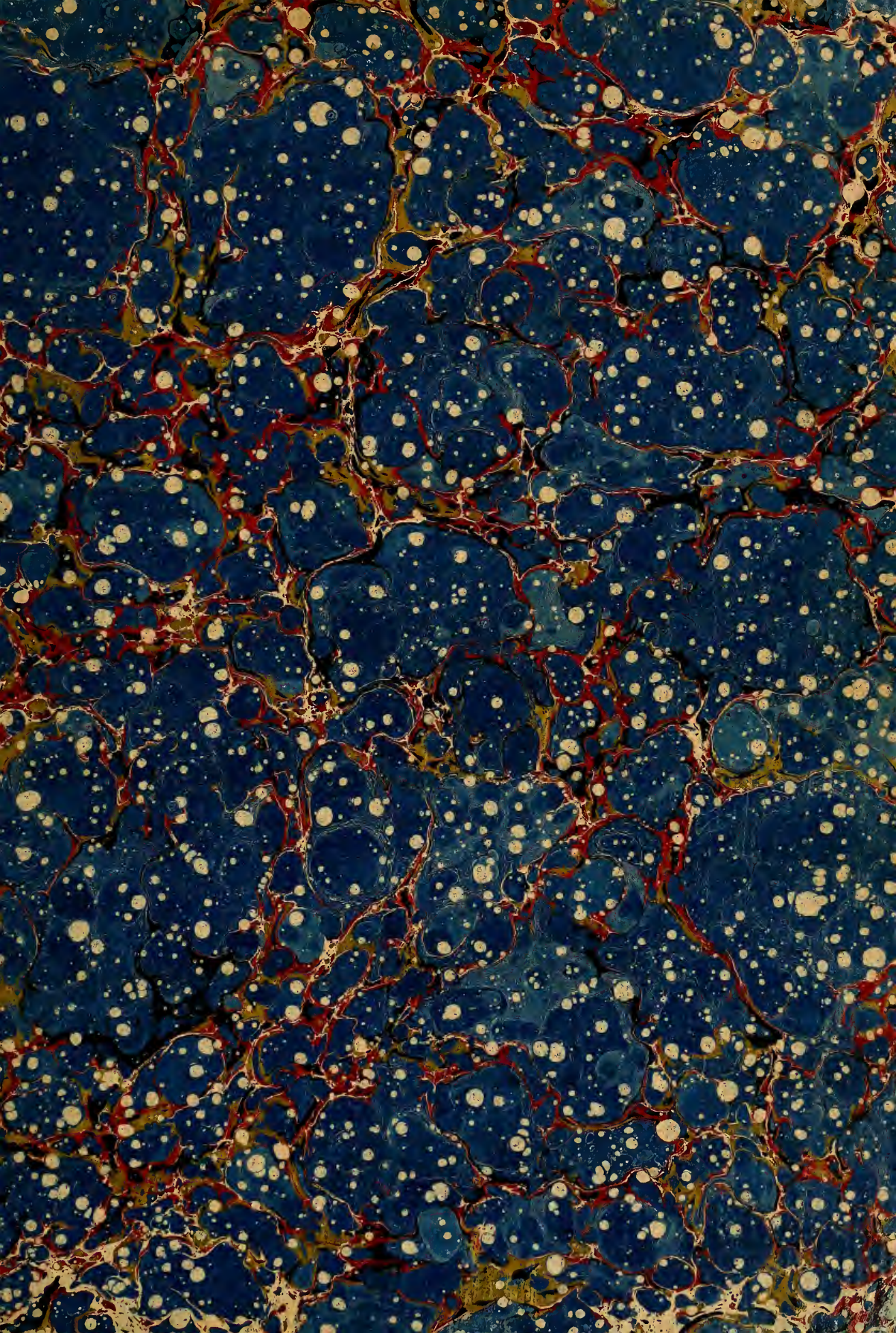

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JOURNAL

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MORPHOLOGY.

VERTEBRATE CEPHALOGENESIS.

II. A Contribution to the Morphology of the Vertebrate Ear, with a Reconsideration of its Functions.

HOWARD AYERS,

Director of the Lake Laboratory, Milwaukee, Wis.

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A. Introductory.

"Es fehlt auf diesem Gebiete nicht an Darstellungen, die Anspruch auf eine vergleichende Anatomie des Gehörorgans erheben; allein sie entbehren eben der genügenden Grundlage."—C. Hasse, *Vergleichende Morphologie des Gehororganes der Wirbelthiere.* 1873, p. 2.

As true as Hasse's words were at the time he wrote them, so true have they unfortunately remained until this time, notwithstanding Hasse's labors, which he characterizes as a "mehrjährigen über alle klassen und selbst über die meisten der einzelnen Familien ausgedehnten Untersuchung, die nach bestem Wissen und Gewissen angestellt ist," and notwithstanding the even more extensive and detailed studies incorporated in the great work published a few years since by Retzius, enti-

tled *Das Gehörorgan der Wirbelthiere.* Feeling the need of a "genügende Grundlage" for the comparative study of the vertebrate ear, in my endeavors to understand the problems of *vertebrate cephalogenesis*, I have sought for, and have, I believe, at last found, the basis from which the characteristic structures of the internal ear take their origin, and the law according to which this development takes place throughout the vertebrate group. The study of the morphology of the internal ear of vertebrates has naturally made much more progress than the study of its phylogeny. In fact, until the publication of Beard's paper on the branchial sense organs, we had no sure basis for homologizing the ear with other sense organs of the vertebrate body. Hence, the internal ear has always been looked upon as a Ding an sich even by those investigators who were constantly endeavoring to gain a clearer insight into its phylogenesis.

In 1883 J. Beard arrived at the conclusion that the vertebrate auditory organ was only a modified portion of the system of superficial sense organs, for which he proposed the name branchial sense organs. Beard arranged the sense organs of the vertebrate head according to their mode of development and their relations to the cranial nerves. He found that the nose and the ear sense organs were related to the surface of the body and the central nervous system through the mediation of the cranial nerves, in much the same way as the sense organs of the superficial system, which he called the branchial sense organs. He did not go further than to state that these two pairs of higher sense organs were derived from branchial sense organs. We shall see further on how far Beard was from a conception of the true nature of the auditory organs. On this occasion, I shall confine myself to a consideration of the auditory organ alone, leaving the nasal organ for a separate paper.

In the paper cited above, Beard says, p. 143: "The auditory organ is, like the segmental sense organs, really a modified portion of the epiblast. Very early in development it becomes shut off in a sac from the epidermis, a condition which only arises later in the segmental sense organs." Beard clearly enough failed to appreciate the significance of the early infolding of the auditory sense organ into its auditory vesicle,

or incipient canal, and he equally failed to see the value of the semicircular canals as evidence of the descent of the auditory organ; for he continues, *loc. cit.*, "the semicircular canals, etc. (meaning thereby, I infer, the utriculus, sacculus, cochlea, and the other parts of the so-called labyrinth) *are clearly secondary complications;* for in every embryo the auditory organ is at first a simple sac, shut off from the epidermis; of which sac a portion of the inner wall consists of two layers of modified epiblastic cells, connected by a dorsal sensory branch of a segmental nerve with the brain." As is well known, the ear is usually inclosed within the head before the surface canal organs are formed; so that, *excepting a few forms*, the direct connection of the auditory organ with the canal sense organs which remain on the surface of the body is not an ontogenetic occurrence.

In sharks, for example, the ear appears long before the other sense organs of the surface of the body, and has sunk below the surface, divided, and begun the production of semicircular canals by the time the organs that are to remain on the surface of the body are apparent. Mitrophanow has recently worked on the development of the lateral line organs in Elasmobranchs. On what species I do not know, since, unfortunately, I have been unable to consult his paper published in Russian. My own observations begun in the summer of 1889 at the Marine Biological Laboratory, Wood's Holl, Mass., on embryos of the Smooth and the Spiny Dogfish (*Galeus canis* and *Acanthias vulgaris*) and an undetermined species of Batoid, probably *Torpedo occidentalis*, leave no doubt that the ear is derived from the sense organs of the lateral line group; for in these species the ear retains its canal connection with the so-called aural group or line of surface organs long after the canal organs and their canals have become well developed.

My observations would perhaps have been fruitless of the main result had I not at that time received a copy of Allis's paper on the development of the lateral line organs of the Ganoid Dogfish.

While reading his account of the manner in which the surface canals are formed in that fish, it was recalled to mind that Van Noorden had described the formation of ampullæ and ear

canals as progressing in a manner practically identical in the Teleost ear. The conviction at once forced itself upon me that since we find in the development identical mechanical processes on the surface of the body and within the ear, resulting in similar structures, viz. the enclosing canals of the sense organs, the ear canals must be genetically related with the surface canals; for my own observations had just shown me that, in two forms at least, the internal ear was a sense organ taken out of a group, the remainder of which is enclosed within the so-called aural canal, near its junction with the occipital and lateral, as I shall describe more fully and with figures further on. Beard ascribed this earlier inclosure of the auditory organ to the fact that the hairs on the auditory cells are concerned in the perception of much finer wave motions than the superficial sense organs, viz. sound waves alone; and he concludes (*loc. cit.* p. 143), "In accordance with, and as a direct consequence of, this function of receiving waves of sound, the auditory organ has been early shut off from the external surface, and has developed accessory structures in the shape of semicircular canals, etc. *Thus its primitive simplicity has been lost.*" I shall endeavor to show that there is no change in the plan of structure of the auditory organ as it grows towards its adult condition, and that there is no more a loss of its "primitive simplicity" than in the case of the superficial sense organs, which, by dividing, produce several or many organs, and where they are *canal* organs, concomitantly bring about the production of a canal complex made up of a number of simple homodynamous units, each related to its fellows according to a simple and symmetrical plan. We need no longer think of the ear as a complicated labyrinthine structure, but rather as a *symmetrical group of organs.*

Although Beard's paper marked a great advance, we were still without clue to the significance of the peculiar and strikingly characteristic structures of the internal ear of vertebrates and the older view which Hasse advanced and defended; viz. that there is a complete agreement between the early stages in the development of the vertebrate ear and the invertebrate auditory organs, and that the former had arisen out of the latter by a transformation of its walls and chambers, was still, if not

accepted by all vertebrate morphologists, at least unchallenged, for the very good reason that there was no basis on which to make any adequate argument to the contrary.

Below I quote Hasse's words expressing his convictions after many years' work in this field of vertebrate morphology, which will apply to his views as advocated by Hertwig in the latter's *Lebrbuch d. Vergl. Embryologie*, Ed. 1888. "Bei immer weiter in der Thierreihe ausgedehnten Unutersuchungen ist es begrieflich, dass manche Ansicht, die man bei den ersten Schritten auf diesem schwierigen Gebiete gewonnen und als fundamental hingestellt, im weiteren Verlaufe der Beobachtungen nicht unbedeutende Modificationen erfährt, dass das, was das eine Mal wichtig erschien, später als Beiwerk sich herausstellt."

It can now be shown that the vertebrate ear is derived from a superficial structure not known to exist among invertebrates, and it consequently follows that the auditory organs of the two groups cannot be genetically related in any more direct or important sense than that involved in the common descent of all animals from some simpler parental form, — a proposition which no one at the present day would for a moment think sufficient ground for establishing the genetic connection of the organs in the two groups. I shall now endeavor to place in clear light the indisputable claims of the canal organ as parent form of the vertebrate internal ear. I do so, however, in the same spirit in which Hasse offered his solution of the problem of the phylogeny of the auditory organ, expressing my feelings in his words. "Glücklich wäre ich, sollte es einem anderen Forscher auf Grund ebenso eingehender Forschung gelingen, die Haltbarkeit oder Unhaltbarkeit meiner folgenden Auseinandersetung nachzuweisen, es hätte dann doch ein kleines Kapitel der Vergleichenden Anatomie der Wirbelthiere einen gewissen Abschluss erreicht, der, um der Morphologie des Menschen ein festes, wissenschaftliches Fundament zu geben, den meisten übrigen dringend zu wünschen wäre." While I believe that we now possess the essentials of the whole history of the vertebrate ear, I am none the less conscious of the extremely slow growth our knowledge of this subject has had, and of its fragmentary state in many details. I should do myself an injustice did I not state that I am cognizant of the fact that some old, and

more new, problems are yet to be solved, but I think they are of secondary importance as compared with the main facts establishing the genesis of the ear in a canal organ group, and its retreat to a place by itself deeper within the head, where it has developed, in its own peculiar and highly functional way, into one of the three main mechanisms controlling our acquisition of knowledge; into one of the principal instruments on which we must depend in our exploration of the vast unknown.

To combine the results of the anatomical investigations with those from the embryological field, and to deduce from this accumulation of facts the general law of development of the vertebrate ear is the purpose of this paper. How well I may succeed I leave time to decide by bringing new and completer knowledge than we now possess of many of the details of the developmental processes, as also of many matters of adult relations of the organ in question which still need elucidation.

For many favors and substantial aid in carrying on my investigations I wish to make grateful acknowledgment to the following gentlemen: —

To Dr. G. D. Ladd and Dr. E. M. Connell for valued assistance. To Professor G. W. Peckham for the use of a fine immersion lens. To Messrs. Cudahy for much valuable material on the mammalian ear. To the director of the Marine Biological Laboratory, Professor C. O. Whitman, and the gentlemen comprising his staff, for very efficient aid in securing the needed marine vertebrates, and also for the excellent library and laboratory facilities accorded me during a short stay in June–July, 1891. And to Mr. E. P. Allis for the gift of living adult and embryonic material of our native marsupial, the Virginia Opossum, which has enabled me to give some account of the auditory anatomy of one member of a group which in this respect is entirely new to science.

The following list includes the forms which have served as the basis for my conclusions. Some species were examined for the solution of one or more doubtful points; but most of them have been carefully anatomized and studied in histological detail as well. As far as possible the material has been studied in the living condition, and I have endeavored by using several methods to reduce the errors necessarily introduced into the

microscopic observations of animal tissues due to changes caused by the killing, hardening, or preserving media. An asterisk in place of a number in the table signifies an undetermined number of ears selected from a large series.

Name of Species.	No. of Ears.	Name of Species.	No. of Ears.
Amphioxus lanceolatus. .	*	Didelphys virginiana . .	4
		Cavia cobaia	4
Ammocœtes	4	Lepus cunniculus . . .	12
Petromyzon Planeri . .	4	Mus musculus	20
" marinus . .	10	" ratus	46
		Canis familiaris	4
Acanthias vulgaris . . .	*	Felis catus	2
Galeocerdo tigrinus . . .	4	Bos taurus	8
Galeus canis	*	Sus scrofa	24
Carcharinus obscurus . .	2	Ovis aries	2
Sphyrna zygæna . . .	8	Homo sapiens	4
Carcharinus glaucus . .	4		
Odontaspis littoralis . .	2	*Embryonic material.*	
Torpedo occidentalis . .	4	Amphioxus lanceolatus .	*
Raja erinacea	*	Petromyzon Planeri . .	14
" ocellata	4	Galeus canis	*
" radiata	2	Acanthias vulgaris . . .	*
" eglanteria	14	Batoid, undetermined .	2
" lævis	2	Salmo fario	*
Dasyatis centrurus . . .	36	" salar	*
Chelydra serpentina . .	4	Felis catus	6
Chrysemys picta	10	Sus scrofa	*
Alligator mississippiensis .	10	Ovis aries	28
Gallopavo americanus . .	6	Bos taurus	15
Gallus domesticus . . .	10	Lepus cunniculus . . .	10
Mimus polyglottus . . .	4	Didelphys virginiana . .	6

B. MORPHOLOGICAL.

"Die ausserordentliche Mannichfaltigkeit in der Bildung der Grundform erklärt sich bei den Organen ebenso wie bei den Plastiden daraus, dass die Anpassungs-Verhältnisse dieser morphologischen Individualität absolut mannichfaltig sind, und dass keine Schranke die Ausbildung des Organs wie der Plastide nach den verschiedensten Richtungen behindert. Dazu kommt noch, dass die verwickelte Zusammensetzung der höhern Organe aus Complexen von niederen, die höchst complicirte Verflechtung von Zellfusionen, einfachen Organen, zusammengesetzten Organen, Organ-Systemen und Organ-Apparaten, alle möglichen Grundformen zu verwirklichen im Stande ist." — HAECKEL, *Generelle Morphologie*, II. 531.

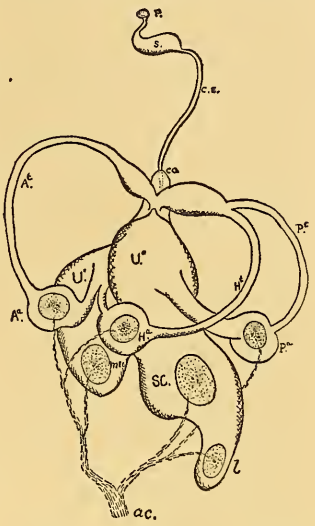
AUDITORY ORGANOLOGY.

1. Stage of the cell colony.	simplest condition and earliest phase of a group of ectoderm cells transformed to sensory cells.
2. Stage of the simple or homoplastic organ.	recognized by its sharp differentiation from surrounding tissue. The surface sense organ.
3. Stage of the compound or heteroplastic organ.	recognized by the division and protection of the organs in canals below the surface.
4. Stage of the organ system.	the phase in which the canal complex, although complicated, remains independent as the functional ear.
5. Stage of the organ apparatus.	the phase in which the canal complex acquires anatomical and physiological relations with other very different structures (*e.g.* the middle and outer ear of higher vertebrates) and with them performs the auditory function.

A description of the internal ear of the Sting Ray (*Dasyatis centrurus*), with comparative accounts of the internal ears of the Electric Ray (*Torpedo occidentalis*), the Hagfish (*Myxine glutinosa*), the Lamper Eel (*Petromyzon marinus*), the Alligator (*A. mississippiensis*), the Mocking-bird (*Mimus polyglottus*), and of Man.

1. Canals.
2. Endolymphatic duct.
3. Maculæ.
4. Utriculus.
5. Sacculus.
6. Lagena (cochlea), of the ichthyopsida and sauropsida.
7. Tectorial membranes and cupulæ terminales.
8. Otoliths otoconie.
9. Perilymphatic spaces of the ear.
10. Continuity of the cerebral and auditory spaces.
11. Mammalian cochlea.
12. Auditory nerve.

As a basis for the account of the vertebrate ear which follows, I shall describe the Elasmobranch ear, using for this purpose, one Selachoid and two Batoid forms, — *Carcharias littoralis*, *Dasyatis centrurus*, and *Torpedo occidentalis* (Pl. I, Figs. 1, 2, and 3, and Cut 1). In Fig. 1 is shown the left ear of Dasyatis, seen from the outside. The most important feature of this ear is the perfection in which the canal plan, or the arrangement of the canals, is presented. The primary channel of communication with the surface parent canal, the *ductus endolymphaticus* (*de.*), enlarges gradually as it sinks into the head. Its enlarged lower end is bifurcate, the median raphe of the utriculo-sacculus separating the primary chamber into two secondary — the permanent or adult ones, which are the utriculus (*u*) and the sacculus (*s*) of anatomists. From the utricular chamber near its junction with the endolymphatic duct is given off a tube, short and relatively narrow, which soon enlarges into the anterior canal complex (*x*); similarly, from the sacculus, but further down on its body, is given off a tube which opens into the posterior canal (*z*). This ear, then, shows very plainly the two chambers usually described as superior and inferior divisions of the ear cavity, or the utriculus and sacculus, and it is perfectly evident that these chambers are not superposed, but placed one beside the other in an antero-posterior direction.



Cut 1. — The left internal ear of *Torpedo occidentalis* dissected out of its cartilaginous capsule, and viewed from the outside. The somewhat diagrammatic figure represents the ear about twice its natural size, as found in a fish five feet in length. A^a, anterior ampulla; A^t, anterior canal; *ac*, auditory nerve; *c.e*, endolymphatic canal; *co*, utriculo-saccular cone; H^a, external ampulla; H^t, external canal; *mu*, macula utriculi, auct.; *l*, lagena and papilla lagenæ; *P*, surface pore of endolymph canal; *s*, its sac; P^a, posterior ampulla; P^t, posterior canal; *SC*, sacculus and its macula sacculi; U' and U'', utriculus and utriculo-saccular chamber.

The utricular and saccular chambers are nearly equal in size in Dasyatis; but in most other Elasmobranch forms, as

well as in all the higher groups, there is a varying disproportion, the sacculus becoming in general the larger of the two chambers.

In the Cyclostomata, as one would expect, these chambers are very nearly equal in size, and in some forms are scarcely separated from one another. In Dasyatis the sacculus is drawn out backwards, downwards, and outwards, into a curved blind pocket (*l.*), the lagena. The utriculus in this species does not show a similar pocket, though it is well developed in some Elasmobranch fishes, and the sense-organ differentiation connected with it variously indicated in many of the higher forms. The anterior canal complex is made up of the two semicircular canals known as the anterior (*ca.*) and the external (*ce.*), respectively, their ampullæ (*aa.*), and (*ae.*) the anterior and external ampullæ, the common ama of the two anterior canals, and the enlargement with which the ampullæ communicate by their short ampullar tubes. The posterior canal (*cp.*) has failed in this species to produce a canal complex; but, as we shall see, its sense organ has by division produced two ampullar sense organs, one of which does not develop an ampulla and canal. The posterior canal, its ampulla (*ap.*), and the tube placing the ampulla in communication with the short canal (*s*), are the parts of the saccular canal.

The endolymphatic duct of Dasyatis (*d.*) is relatively large, and preserves the continuity of the lining coat of the internal ear with the surface of the body from which it sprang, and thus in a certain sense the superficial position of the auditory sense organs. When we recall the well-known facts relative to the location of the lateral line organs, — placed below the surface of the skin in canals, in pits, or at the bottom of deep depressions in the surface of the body in many species, or going still further to occupy channels hollowed out in the subdermal cartilage, and more or less complete canals formed in the dermal bones and scales of the body in other forms, — we perceive at once that the position of the ear within the skull is different from that of its relatives at or nearer the surface of the body, *merely in the degree* of removal and the extent of the modifications induced by such removal from the surface.

The utricular and saccular chambers of the Torpedo ear (Fig. 3) and of the Carcharias ear (Fig. 2) are quite similar in

shape. The separation of the two chambers (Cut 1) from the median portion (inner end of the endolymphatic duct) is not so complete and typical as in the case of the Dasyatis ear. The two chambers appear as appendages of the median much-enlarged portion, and their relation to the median raphe of division is masked somewhat by the size and position of the median chamber. The enlarged end of the *surface canal*, the so-called endolymphatic duct, forms in these ears the utriculo-sacculus proper, which is a relatively large pear-shaped or subconical sac. Its walls are perforated by holes, one placed on the anterior inner face, the other on the posterior inner face of the median sac. The median chamber forms about one-third of the ear sac of the Torpedo, and the utriculus and sacculus appear to spring out of its lower anterior, inner and lower posterior, inner faces, respectively. The stem of the pear is formed by the long endolymphatic duct, which leads off from the funnel-shaped enlargement at the small end of the pear. This part corresponds to the *aqueductus vestibuli* of other vertebrate forms, and is clearly the basal portion of the endolymphatic duct, which, remaining undivided, does not so openly disclose its nature as does the homologous part in the Sting Ray (Pl. I, Fig. 1).

In the Torpedo the utricular and saccular evaginations, which have resulted in the formation of the semicircular canals, communicate at three points with the auditory sac. They are placed, as an inspection of Cut 1 shows, one near the anterior border of the utriculus, one near the posterior border of the sacculus, and one near the apex of the cone-shaped chamber common to both the utriculus and sacculus. The first of these openings is a "half-pore," as defined by Allis, and represents the original pore left by the canal formed over the anterior ampullar sense organ. The canal leading outwards from this pore soon splits into two, one of which leads into the external ampulla. This splitting of the canal was induced during development by the division of the anterior ampullar sense organ, and resulted in providing the offspring of the parent organ with a canal of its own, which, however, does not, as in some species, acquire a separate opening into the utriculus, but uses the parent canal for such communication. The second opening is that of the saccular ampullar organ, or that of the posterior canal, which in

this species has budded off a sense organ.[1] The third opening is used by all three canals, whose amal ends here unite into the common pore opening into the remnant of the primitive utriculo-saccular chamber. There is a much greater variation among the vertebrate forms yet studied in the manner in which the amal ends open into the auditory sac than is the case with the ampullar ends, and this variation is due in large part to the mechanical influences at work, shaping the auditory canal complex during its early stages of development. Each of the canals at its amal end is swollen out into a sub-oval sac, which I shall designate the ama (from the Gr. *ama*, water-holder). This second enlargement of the canals at their upper (outer) ends deserves special mention from its wide distribution among vertebrates. It is in no way related to sense organs, and is always lined by a pavement of epithelium. It occurs in some or all of the canals of the majority of Elasmobranchs; has been figured but not specially described for Teleosts; is known to occur in the human ear, and other mammalian forms in the adult stage, though much more distinctly marked off during the fœtal life of these forms, when the double curvature of the canals, so constant a feature of the fish type of canals, is also well developed.

In the Sting Ray (Pl. I, Fig. 1) the canal offshoots from the utriculus and sacculus differ materially, as has been indicated in their relations to the central parts of the canal complex. Owing, in the first place, to the greater simplicity of the central chambers in Dasyatis, the canals do not open into the undivided median part, although there is an approach to this condition in the position of the connecting tube of the anterior canal complex. The canals of each chamber communicate with that chamber alone, and in this respect preserve their primitive relations.

CANALS.

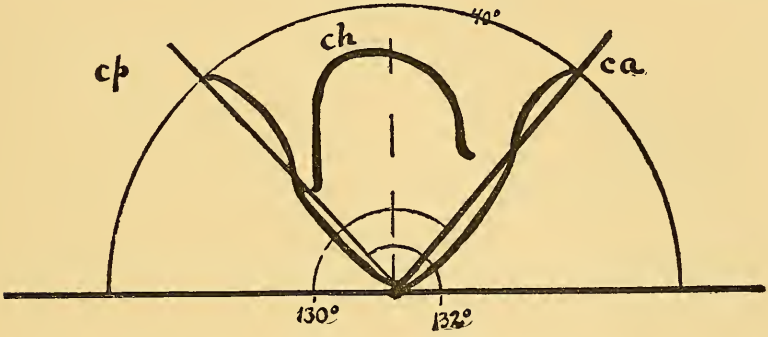
In *Torpedo* the semicircular canals measure 1.4 mm. in diameter, the actual length of the largest canal (the anterior) being 5.2 cm. Each canal lies in a relatively large channel, hollowed out in the cartilaginous capsule. These canals are by

[1] The position of this organ is shown in Pl. I, Fig. 3, *ab.* and *rl. ab.*

no means semicircular in shape, nor are they placed at right angles to each other.

The planes in which the canals for the most part lie are not parallel with the three planes of the animal's body; viz. the sagittal, transverse, and horizontal respectively.

The extent of the variations from these three planes are shown in Cuts 2–6. The anterior vertical canal *ca.*, as seen from above, bends caudad in its distal portion, and cephalad in its proximal portion; its plane cuts the sagittal plane of the body at an angle of 50°. The angle included between it and its fellow, the posterior vertical canal (*cp.*), is not 90°, but only 82°. The angle at which the posterior vertical canal cuts the sagittal axis of the body is consequently 48°, and it does not coincide with any transverse plane passed through the body. It is thus seen that



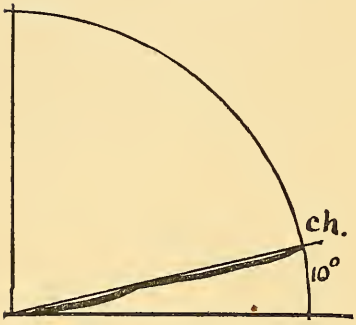
Cut 2. — A projection of the semicircular canals of the ear of the *Torpedo occidentalis* on the horizontal plane, to show their angular relations to the vertical (sagittal) plane.

the vertical canals do not lie in planes parallel with two axial planes of the body, respectively, the sagittal and the transverse, as is commonly supposed. The so-called horizontal canal, or, as I prefer to designate it, the external, does not lie in a plane parallel with the horizontal plane of the body, but always, as I have found it, inclined in two directions to that plane. The usual arrangement is presented by the Torpedo where the plane of this canal inclines downwards and forwards from the horizontal.

On comparing the various canal-forms found among vertebrates, one is struck by the great variety presented. The

size, the shape, the position of the parts of the canalar arch with respect to the three planes of space are subject to extensive variation.

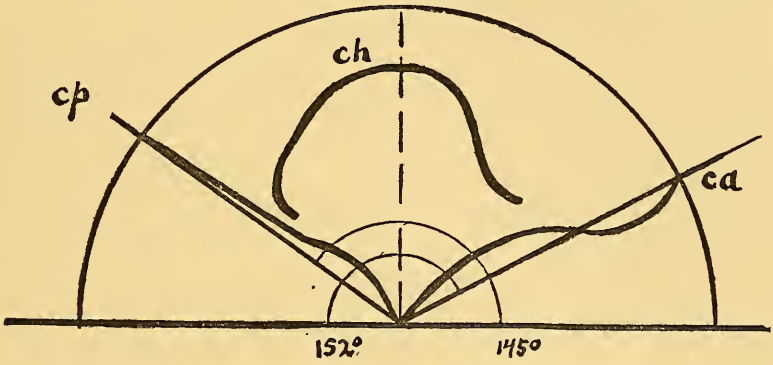
We have just seen the character and degree of these variations in Torpedo. I can do no more here than to state that every species of vertebrate has its own peculiar variation above and beyond the individual differences. As regards the length of the canals, they vary from about 1 mm. in length, as in the smaller species, especially of the higher vertebrates, to 13 cm., as in the case of a shark measuring seven feet in length. In our recent sharks the canals do not, perhaps, exceed 20 cm. in length in any case. In the seven-foot shark, with canals 13 cm. in length, the largest teeth measured only one inch across the base. In nearly related extinct forms with teeth measuring five inches across the base, if the same proportion held good between their canal and teeth measurements, — and there is every reason to suppose that such was the case, — these enormous extinct forms must have had canals at least 65 cm. in length. That such angular variations from the commonly understood relations of the canals, as I have described, are of frequent occurrence has long been known, but not much, if any, allowance has been made for the almost universal failure of the canals to come up to the theoretical standard, and no notice has been taken of the very much modified type by the speculative physiologist. Hasse described in 1868 (117) the frog's ear canals in great detail. He found that the external canal projects upward from the horizontal plane at an angle of from 40° to 55°, and the anterior and posterior canals are nearly as much out of the sagittal and transverse planes. Hasse had already pointed out the general law, that the ampullæ and the canals are placed obliquely to the planes, whose names they bear, and he says further (*loc. cit.* p. 12), "Es ist demnach nicht vollkommen richtig, wenn wir von



Cut 3. — A projection of the horizontal canal of the same ear on the sagittal plane, to show its relation to the horizontal plane.

einem horizontalen, einen frontalen oder sagittalen Bogengang sprechen. Auch beim Menschen kommen solche abweichungen von den verschiedenen Ebenen, und zwar konstant, vor," u.s.w.; and he cites the passage in Henle's *Splanchnologie*, dealing with measurements of the angles of divergence. Henle gives 10° divergence from the assumed normal planes as the most constant (normal) condition in the human subject.

In the Sting Ray the posterior canal is almost entirely separated from the sacculus, and has no relation to either of the remaining canals. Its means of communication with the sacculus is a very small tube, given off from the canal above the ampulla, as already described (Fig. 1). The same condition of separation has been figured by both Hasse and Retzius for



Cut 4. — A projection of the semicircular canals of the ear of *Dasyatis centrurus* on the horizontal plane, to show their angular relations with the vertical (sagittal) plane.

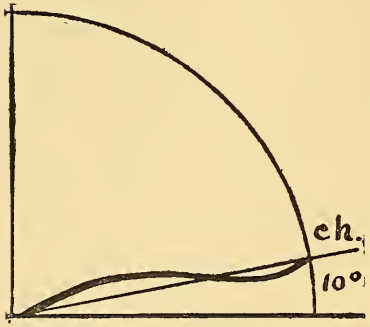
other Elasmobranch forms, and is one of the characters of special importance, which we shall need to consider again.

The anterior and external canals, which unite into a common tube (Pl. I, Fig. 1) above, are only connected with the utriculus by a very small hollow stem.

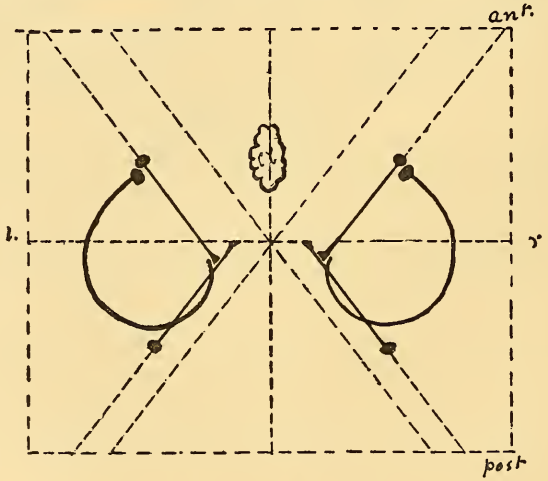
It is thus apparent that the channels, placing the utricular and saccular canals in communication with their respective chambers, are very much simpler than those present in Torpedo (Cut 1).

The separation of the posterior canal progresses in some instances to a *complete* separation from the sacculus, the communicating tube becoming closed and persisting as a solid

thread between the two structures. The endeavors of anatomists to arrange the canals under a common type have not proved fruitful, for the reason that no such relations exist between the canals and the other parts as has been supposed. Each canal is an individuality whose characters, so far as shape, size, and spatial relations, are not connected in any special way with the corresponding characters of its neighbors. In its development each canal takes such shape and relations to other parts as its surroundings permit. They are *not developed as specially functional structures*, and their relations may well be a matter of no account to the animal. As we shall see further



Cut 5. — The horizontal canal of the same ear projected in the sagittal plane.

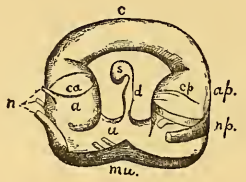


Cut 6. — A projection of the semicircular canals of a *Galeus canis* five feet in length on the horizontal plane, to show their angular relations to the sagittal plane and to each other. No allowance is made for the curvature of the canals in their proper planes. Natural size.

on, two of them are related as parent and offspring, descended from the utriculus, while the remaining posterior canal is a descendant of the sacculus.

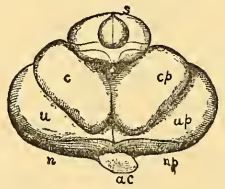
The canals among the Elasmobranchs have retained more of their primitive relations to the utriculo-sacculus than those of any other group, except the Cyclostomes. This is due to the fact of the greater separation of the canals by the presence of the double-chambered utriculo-sacculus between them, which in the higher forms becomes more and more indistinct and reduced by the migration of the main portion of the sacculus ventrad of the utriculus, its upper portion only being left in connection with the utriculus.

Hasse and Retzius both describe the ear of Myxine as possessing but one semicircular canal, which they term the vertical canal, and Retzius further regards the single canal arch in Myxine as the homologue and forerunner of the utriculus of the Gnathostome vertebrates. Since the single tubular arch in Myxine rises at either end out of an ampulla, just as the anterior and posterior vertical canals of all other forms take their origin, and since the ampullæ of the two ends of the canal in Myxine are related to the utriculus as regards the anterior ampulla and the sacculus as regards the posterior ampulla in exactly the same manner, both with respect to the walls of the chambers and the sense organs contained, as they are in all forms above the Hagfish; and finally and especially since the anterior and posterior roots of the auditory nerve innervate the anterior and posterior ends of the canal respectively, it is an unavoidable conclusion that either the so-called single vertical canal in Myxine is a product of the fusion of the two verticals of other forms, or that it represents a primitive undifferentiated condition. Especially so, since its near relative Petromyzon has two canals. These two canals, however, unite with each other before opening into the utriculo-sacculus, and it is only the common tube thus formed which lies between the point of union and the



Cut 7.—The right internal ear of the Hagfish (*Myxine glutinosa*), seen from the inside or cerebral face. Figure after G. Retzius. The figure represents the ear somewhat enlarged, and does not show the shape or exact positions of the contained sense organs. *a*, anterior ampulla; *ap*, posterior ampulla; *c*, anterior and posterior canals; *ca* and *cp*, ampullar ends of the same; *d*, ductus endolymphaticus; *mu*, macula utriculi et sacculi; *n*, nerve branchlets; *u*, utriculo-sacculus; *s*, sacculus endolymphaticus.

utriculo-saccular wall that is present in Myxine. An examination of the type figure for the Cyclostome ear (Pl. IX, Fig. 2) well illustrates the character and extent of the difference between Myxine and Petromyzon in this respect. The semicircular arch of Myxine is, then, composed of the anterior and posterior vertical canals of the Gnathostome vertebrate ear. It is hardly necessary to add that the argument of degeneration based in part on this peculiarity of the internal ear of the Hagfish is not sustained by the facts in the case. Retzius states that if the single canal of Myxine is homologous with any part of the higher vertebrate ear, it must be with the utriculus (according to the old conception of the extent of this chamber). Retzius says that it cannot be the equivalent of the vertical canals of other forms. Of the third or external canal Retzius was likewise led to conclude that not a trace of it is present; but just as in higher forms the *macula neglecta* or *abortiva* does not develop a canal and ampulla, although it has its discreet nerve branch, so here, although ampulla and canal are not developed, still the sense organ is in some degree separated from its parent, the anterior ampullar organ, for it receives a discreet branch of the ampullar nerve, and relying upon the nerve distribution there are in Myxine as in Petromyzon indications of the future secondary canals. The endolymphatic duct is present and sometimes bifurcates in its distal portion. This bifurcation is probably a remnant of a previous double condition.



Cut 8.—The right internal ear of a Lamper Eel (*Petromyzon fluviatilis*), viewed from its inner or cerebral face. The figure after Retzius. *ac*, auditory nerve; *c*, anterior canal; *cp*, posterior canal; *n*, ramus utricularis; *np*, ramus saccularis; *u*, utriculus; *up*, sacculus; *s*, ductus et sacculus endolymphaticus.

The canals in the Lamper Eel are well developed, but on account of their close application to the surface of the utriculosacculus they are not apparent as separate canals from the outside. In order to arrive at an adequate knowledge of their size, shape, and mutual relations, it is necessary to study them in sections of the ear. They are, however, fully separated from the utriculus and sacculus for at least part of their length, and in the large Lamprey one is able to pass a sound between the canal and main chamber

on removing the perilymphatic connective tissue. The anterior vertical canal springs from the utriculus, and curving upward, outward, and backward unites with the posterior vertical canal, which, after arising from the posterior end of the sacculus and passing upwards, forwards, curving as it does so, first outwards, then inwards, meets its fellow above the median portion of the utriculo-sacculus. They are somewhat flattened in section at their ends, and open by wide mouths into the middle divisions of their respective ampullar chambers. In the middle of their course their cross-section is circular. Seen from the inside of the utriculo-sacculus, the canals present the appearance of short archways leading from the large ampullar chambers, below where they freely communicate with the utriculo-sacculus up to the narrowed ends of these same chambers, into which they again open. The endolymphatic ducts, for Petromyzon possesses a pair of them, both proceed from the utriculo-sacculus to the cranial cavity. One of them opens into the lower posterior face of the utriculus, while the other perforates the median triangular plate between the utriculus and sacculus, with a tendency to open more into one chamber than the other, and it is sometimes the utriculus and sometimes the sacculus with which it most freely communicates. The last-mentioned duct contains a large sense organ (Pl. I, Fig. 14, and Pl. X, Fig. 2).

In the Alligator the canals have begun to lose their importance. Passing from the Cyclostomes, where they begin their differentiation, through the Elasmobranchs and true fishes, where they reach their greatest perfection, we find them among the Amphibia and all the air-breathers gradually losing their prominence relative to the other parts of the ear, especially the saccular region from which the lagena has begun its growth.

I think it is not necessary to enter into a detailed description of the semicircular canals here, although there is much of value which might be recorded of these canals in the Sauropsid types.

In *Mimus* as a representative of the avian type and in the mammalia as represented in Man, the canals are characterized by an increased delicacy and regularity of outline, seldom showing those modifications of form so apparent in the fish types. In size the canals undergo considerable variation, and on the whole, as said before, they are evidently of less importance to the auditory economy than in the Ichthyopsida. In Mimus the

canals are not so large as those of the pigeon, have nearly the same diameter, but have decidedly different shape and individual peculiarities of spatial relation, resembling very closely in these things the song thrush (*Turdus musicus*). A close agreement between these two forms was to be expected. The anterior ampulla of Mimus is much smaller than either the posterior or the horizontal, and of these two the former is the larger.

ENDOLYMPHATIC DUCT.

In the Torpedo the endolymphatic duct is the long tube which runs from the funnel-shaped cap of the utriculo-sacculus through the muscles, skull, and skin to open out on the dorsal surface of the head just in front of the so-called aural line of canal organs.[1] It does so by means of a funnel-shaped depression in the skin. Just beneath the skin it swells out into a sac-like enlargement which is usually filled with otolithic crystals. The communication thus kept up between the sea-water and the internal ear renders the liquid contained in the ear very like the sea-water, and analysis gives only a trace of organic matters, such as mucin and other albuminoids. The sharks preserve this duct in its simplest form; *i.e.* in its most primitive form. In the remaining Ichthyopsida and in the Sauropsida the organ is much reduced and its course of development changed. In the forms just named it does not open upon the surface of the head, but it may communicate with the lymph spaces about the central nervous system. In other forms it ends blindly in a saccular enlargement, usually after having penetrated into the cranial cavity, and finally it may be present as an inconspicuous protuberance on the dorso-median portion of the ear sac.

When it communicates with the brain spaces, its inclusion within the skull is due to its being inclosed by the membrane bones during development, — the bones which normally protected its parent organs. In this connection I wish to call attention to some modifications of this duct and of the utriculo-

[1] In some Elasmobranch forms the endolymphatic duct opens on the surface *behind* the aural canal. In all species the tube pierces the skin obliquely, and is here much contracted; the opening, whether slit-like or a funnel-shaped depression, is usually situate on the top of a dermal hillock.

saccular walls which possess great interest from their unusual relation to other organs of the body, particularly the central nervous system, but whose morphological as well as physiological significance is still entirely unknown.

These structures are known as the otolith sacs of the brain and spinal cord and as the chalk sacs covering the ventral surfaces of the spinal ganglia in many Amphibia. The endolymphatic sac is otherwise peculiarly modified, as in the oft-mentioned Phyllodactylus, where it forms a large flattened shoulder sac lying beneath the skin, partly hidden by the muscles.

That we have to deal in many of these cases with outgrowths of the primitive auditory vesicle is evident, but we do not yet know sufficient of their development, adult structure, and relations to other organs to hazard opinions as to their functions. We are very much in need of further knowledge of these structures, and the subject will doubtless well repay the investigator.

The endolymphatic duct, which in man is bifurcate at its lower end, serves to unite indirectly the two primary divisions of the ear. This condition is now seen to be a remnant of the early relation of these two chambers, as may be deduced from the account of the ears of Myxine, Petromyzon, and Dasyatis.

A comparison of the ears of Myxine, Petromyzon, Dasyatis, Torpedo, and Man clearly shows the connection of the duct with the utricular and saccular chambers to be a fundamental condition, and not a secondary acquirement, as has hitherto been held.

In the preceding account I have mentioned two tubes in the Cyclostome ear, and described them as the endolymphatic ducts. In Petromyzon (*P. marinus* and *Planeri*) the second tube, from its position and connections, is equally entitled to be classed as an endolymphatic duct. It has been figured and described by only two authors, and in both instances inadequately. The relative size and the position of this second tube is shown in Pl. X, Fig. 2, *D.e.s.* I shall designate this tube the utricular duct, or the *Ductus endolymphaticus utriculi*, while for the other tube I propose the name *Ductus endolymphaticus sacculi*, or saccular duct. The saccular duct is the larger of the two, having a greater diameter, a larger end, and a somewhat greater length, while the utricular duct, although nearly as long, tapers to its end, which is only slightly enlarged. The utricular duct leaves the

utricular chamber cephalad of the median line as a tubular evagination from the lower, posterior lateral face, deep within the utriculo-saccular groove, but it is much less a median structure than the saccular duct which leaves the utriculo-saccular chamber almost immediately from the line of union of the two chambers. Both ducts run upwards (and near each other in so doing), inwards, and backwards, piercing the cranial wall side by side, and end projecting into the subdural lymph space. The foramen giving passage to these ducts lies above and is entirely unconnected with the large foramen for the passage of the auditory nerve. It is much smaller and is nearly filled by the two tubes, the remaining space being occupied by the perilymphatic tissue. The saccular duct is lined by a pavement epithelium throughout, except where the sense organ furnishes a columnar epithelium.

The importance of this question has led me to search for the second duct among the Gnathostomes, and if one can rely on the literature of the subject, two endolymphatic ducts are present in some of the Elasmobranch fishes.

Hasse found (and in this he agrees with Ibsen) a bifurcated endolymphatic duct, the main branch of which arose from the inner wall of the sac, while the small branch arose from the upper inner wall of the *Recessus utriculi* and opened into the larger tube. Hasse, however, was in error in regard to the extent of the tube.

I have not seen the bifurcate endolymphatic duct, described by Hasse for the species which he studied, but the two endolymphatic tubes observed by E. H. Weber, I have found beautifully developed in Sphyrna zygæna, and there is not the slightest doubt as to their occurrence.[1] Although I have never found two open endolymphatic ducts, except in the Hammer-head Shark, I have frequently found in the place one would seek for a second tube, a rod, apparently solid, reaching from the sacculus

[1] Breschet (40, 1838) describes the main facts about the endolymphatic ducts as observed by him in the following words: "Sur la côte interne du bulbe auditif, on voit deux cavités dirigées de haut en bas et recourbées en arrière vers leur extrémites. Ces conduits se rétrecissent près de la peau exterieure et semblent être bouchées en cet endroit par du tissu cellulaire; ils aboutissent à la partie moyenne et supérieure de la tête ou ils s'ouvrent par deux petits orifices."

"Dans le milandre (*Squaulus galeus*, *L.*), il y a ce qu'on nomme improprement des *évents:* ceux-ci s'ouvrent par des petits orifices sur la tête, près de la ligne médiane

(a prolongation of whose wall it seems to be) to the roof of the auditory chamber, which, as the reader will recall, is formed by the tympanoid sheet of connective tissue (the perichondrium) closing the posterior auditory foramen. Further than this I have not been able to trace this cord, and of its ontogeny I know nothing. But when we recall the two tubes in Petromyzon with their remarkable relation to the utriculo-sacculus in connection with the nerve supply of at least one of them, the development of the sense organs of the ear in Petromyzon, together with the entirely similar nerve supply and development in the Gnathostomic forms, — when we recall these and other related facts, the conclusion is near at hand, that the double endolymphatic ducts so constant in Petromyzon, occasional, if rare, in Gnathostomes, represent an ancestral condition, and they constitute most valuable evidence in tracing the phylogeny of the ear.

Breschet (40, 1838) discovered in the sturgeon's ear a small body attaching the membranous sacculus to the cartilaginous wall. He considered this body the homologue of the ear bones of higher forms, and described its structure as osseus, naming it the stapes of the sturgeon.

Retzius (237, 1881) confirmed Breschet as to the fact of occurrence, but was inclined to doubt the justness of homologizing this body with the auditory ossicles of higher forms. Retzius could offer no explanation of its occurrence. This body in the

et au-dessus des organes auditifs; ces petits pertuis conduisent dans un canal qui s'élargit considerablement en descendant, il a sa plus grande largeur à peu près au niveau du cerveau. Le canal se trouve sur la côté interne du bulbe auditif, et n'est séparé de la cavité crânienne que par une mince lame cartilagineuse. Vers la base de la cavité crânienne il se recourbe en arrière. Ce canal est tapisse d'une membrane, et voici comment il se comport à l'égard de l'organe auditif: 1. il communique avec l'interieure du bulbe auditif, au moyen d'une orifice d'une ligne de diamètre; cet orifice est en dehors et se dirige de haute en bas; 2. il communique (en s'y terminant inférieurement) avec le canal semi-circulaire *postérieure* [italics mine,] en se continuant avec l'ampoule inferieure de celui-ci. D'apres tout cela, il me semble que l'*évent* de ce poisson n'est autre chose que l'aqueduc du vestibule des animaux superieures."

Our author found in Rays that "cette cavité auditive a deux sortes de communications avec l'extérieure: 1. elle présente ce que, dans l'anatomie de l'oreille, on appelle une fenêtre; 2. une communication se voit entre la cavité du labyrinthe membraneux et l'extérieure. La première, fermée par une membrane, est en rapport, par sa face interne, avec la cavité du labyrinthe cartilagineux, contenant la *perilymphe*. La seconde, plus remarquable encore et plus isolite, établit une voie libre entre le *sinus median* et le milieu dans laquel vit l'animal."

sturgeon is in all probability — indeed, I think there can be no doubt about it — identical with the cord which I have described above, and would consequently represent the saccular endolymphatic duct. Embryology will very likely reveal the whole truth.

The first anatomist to record the structure of the so-called oval (or round) window of the Elasmobranch ear was Scarpa, who (250, 1789) described two round depressions which appear on the top of the occipital region after removing the skin. The floors of the shallow depressions are formed by thin connective tissue membranes, which he likened to tympanic membranes. Removing these, the membranous ear is exposed, or, as he thought, the vestibular chamber alone.[1]

E. H. Weber (285, 1820) described with great exactness and detail the Batoid ear (*Raja miraletus*, *clavata*, *torpedo*, and *aquila*).

He discovered two external openings (endolymphatic ducts) for each ear of these animals. The anterior of these corresponds to the endolymphatic duct of other authors, but according to Weber, opens out on the surface, after enlarging into the saccus endolymphaticus, *through three tubes*. These pores I have figured on Pl. I, Fig. 13, for *Raja ocellata* of the New England coast. The pores of the aural canal also occasionally communicate with the distal section of the endolymphatic duct. In the Torpedo, however, Weber found only one canal leading outward from the endolymphatic sac (*loc. cit.*, Pl. IX, Figs. 75–86).

Recently G. B. Howes (144, 1891) has advanced the theory that the thin membrane filling the *fenestra vestibuli cartilaginei*, as described by Scarpa, is the first trace of the vertebrate tympanum, and he calls attention to the presence of a mass of "homogeneous semifluid stuff" which occupies the space between the skin and this so-called tympanic membrane.

The homology which Howes seeks to establish cannot be maintained. The fenestræ rotunda and ovalis of the mammalian ear

[1] In Scyllium, Cestracion, and Chimæra, where this region is covered deep under muscles, these openings are small, and may be entirely absent. Among the skates the openings are usually large and the membrane well developed. It is worthy of note that in no case does the skin show any modification (as greater thinness) over the foramen and its tympanoid cover as occurs over the true tympanum of other vertebrates.

have no genetic relationship with the so-called fenestra ovalis (or rotunda) of the Elasmobranch ear. The latter is the result of the closing of the foramen of passage of the saccular endolymphatic duct or surface canal, while the former are new formations. The membrane which closes the foramen in the Elasmobranch cannot then be a true tympanum, for the latter is a product of the closure of a gill cleft, and belongs to an entirely different territory of the head.

Long after the rest of the ear is inclosed in a cartilaginous case the endolympathic duct of the mammal ear leads out to the surface of its capsule through a foramen in the cartilaginous wall and ends in a semi-gelatinous tissue just as it does in the adult shark. Boettcher (31, 1869) describes this condition in the 2.8 cm. embryo sheep in these words: "Während, wie bemerkt, die halbzirkelförmigen Canäle ganz, die Anlage der Vorhofssächen und des Canalis cochlearis von aussen und unten von knorpligem Gewebe eingeschlossen sind, liegt der Recessus labyrinthi in einer bindegewebigen Umhüllung die sich aus spindelförmigen Elementen mit spärlicher Zwischensubstanz zusammensetzt. Diese spaltet sich an Durchschnitten mit den oberen zwei Drittheilen des Recessus labyrinthi von der knorpelig consolodirten Kapsel des Gehörorgans leicht ab. Zwischen dem Recessus und der letzteren verlaufen Blutgefässe in der Richtung des Canals zu dem weiten klaffenden Sinus petrosus inferior, welcher in dem Winkel zwischen dem Blindsack des Recessus und der Knorpelkapsel des Labyrinths beiden Theilen hart anliegt."

I have not studied the development of the mammalian *fenestra rotunda and ovalis* sufficiently to enable me to give an account either of the causes which have been active in their production or of the histological details of the processes. They lie outside of the province of this memoir, since they have no structural connection with the sense organ canals.

Boettcher (31, 1869) gives the following account, from observations on the adult cat (*loc. cit.* p. 41): "Der Recessus labyrinthi underscheidet sich gerade dadurch wesentlich von den übrigen Theilen der Labyrinthblase, das sich in seiner Umgebung kein accessorischer Hohlraum entwickelt. Der epitheliale Canal verwächst allseitig mit seiner Umgebung und erscheint nach erfolgter Verknöcherung in der Felsenbeinpyramide von dem

Periost des knöchernen Aquaductus vestibuli und an seinem hinteren blinden Ende von der Dura mater dicht umschlossen." A condition of things which I have often observed, and which, when we recall the embryonic condition in connection with the permanent arrangement in sharks, receives its explanation.

The semi-gelatinous mass of the embryo, which occupies the foramen for the ductus endolymphaticus is ultimately obliterated, being encroached upon by the ossifying membrane bones and closely invested, since the whole of these structures lie within the dermal zone. The perilymphatic spaces are confined to those parts of the canal complex which retain the primitive chondrocranial capsule, to which the ossific processes are confined.

The sense organs of the internal ear have not been studied from the standpoint of their descent from superficial canal organs, and I think this in many ways fortunate for my demonstration. For we find in the literature numerous accounts of the development of the auditory nerve-end organs in several vertebrate forms, which agree in a remarkable manner with the accounts given of the development of the canal organs. We are thus provided with a valuable fund of knowledge that is certainly entirely unprejudiced and thoroughly independent. This evidence I shall give further on. Just here I shall give an account merely of the shape of these sense organs and of their position within the ear cavity. The so-called *maculæ* all lie within the larger cavities of the ear, but are not separated from the *cristæ* by any sharply defined characters such as would seem to be indicated by the older accounts of them and by the terminology applied to them.

They are usually oval bodies, and are seldom irregular in shape. They may be circular, or drawn out into bands. They lie flat upon the walls of the ear chambers in which they are placed, and do not show the tendency to elevation observed in the cristæ or ampullar sense organs. The hair cells are thus placed on a level floor, and none of the hairs project beyond their neighbors, unless by reason of superior length. The utricular end organ — *macula acustica utriculi* — of many Elasmobranch species, and from here on throughout the remaining members of the vertebrate group, frequently appears in part as a serially arranged patch or row of sense organs, — indeed, such is

the morphological value of the greater portion of the so-called *macula utriculi*, the remaining part being the parent organ. Although arising by the division of the utricular sense organ and at first having the same general form and mural relations, the cristæ soon begin a growth which makes them quite distinct from these latter. This process of growth is caused by the peculiar mode of development of the ampullæ and by the manner in which the nerve branch enters the wall to distribute its fibres to the sensory cells. The ventral ampullar wall is pushed upwards into the ampullar cavity in the form of a transverse ridge or crest, in connection with the ingrowth of the nerve. The hair cells cover this crest, and are consequently most advantageously placed for the reception of wave motions of the endolymph. The canal sense organs of the surface of the body are in many species located on crests or elevations in the manner just described. The conclusion I wish to draw from the facts recited is that the *cristæ acusticæ* of the ampullæ retain their original form, while the maculæ have lost the tendency to assume the crest shape, *i.e.* the tendency to acquire an elevated position above the surrounding adjacent surface. In Myxine and Petromyzon the so-called *macula acustica communis* possesses more than usual interest for the morphologist from the fact, first noted by Retzius, that, owing to its position within the ear cavity, and also to the nerve branches which supply it, the sensory surface is with propriety spoken of as composed of several sense organs. Retzius was led by the nerve distribution to think that perhaps the posterior branch of the anterior root was the homologue of the ramus utriculi, and that the anterior branch of the three branches of the posterior root was the homologue of the ramus sacculi, while the whole of the third branch was the ramus ampullæ posterioris, the second branch being the ramulus lagenæ. The table given in connection with the account of the distribution of the auditory nerve in Myxine explains more fully my classification of the nerve branches, and particularizes the differences between it and Retzius' classification.

Corti's organ, as such, appears for the first time among the mammalia, and it progresses gradually in its complication toward the higher forms. It is derived from the so-called lagena of the Ichthyopsoid and of the Sauropsoid forms lower

than the alligator. The lowest mammals, Echidna and Ornithorhynchus, show most decided reptilian characteristics, and they may be said with truth, I think, to possess a well-developed lagena, or the Anlage of a cochlea, as well as the organ of Corti. One great peculiarity of the cochlea is the spiral twisting it has acquired during its phylogeny, and which is repeated in each ontogeny. Since the cochlear sense organ originates as a canal sense organ, and its adult condition is directly traceable from such primitive conditions, we must conclude that the organ of Corti is a canal organ derivative, and that in the adult condition it either represents a chain of sense organs closely connected, or it is a single but much elongated organ.

When one studies the condition of the sense organs of the vertebrate ear, as found, for instance, in Torpedo and Dasyatis (Cut 1 and Pl. I, Figs. 1 and 3), the equal division of nerve end organs between the two branches of the auditory nerve, the anterior and posterior respectively, is perhaps the most fundamental and important relation presented. I am sure, however, that we cannot overestimate the fact that the *ampullar organs* are here sharply divided into two groups, each group communicating with its own division of the utriculo-sacculus, the anterior consisting of a pair of ampullar organs formed by the division of the anterior ampullar organ of the Cyclostome type, the posterior remaining a single organ so far as the production of an ampulla is concerned. Nor must the relation escape us that the anterior group is connected with the utricular organ, while the posterior group is as certainly connected with the saccular organ. (See type figures, Pl. IX, Figs. 2 and 3.)

The ampullar sense organs not infrequently divide without causing a division of the ampulla and canal, but in all such cases we find the supernumerary organ still inclosed in the ampulla with its parent, though supplied by a distinct branch of the ampullar nerve. The offspring is usually removed a short distance from the parent and may lie anywhere between the utriculo-saccular chamber and the parent ampullar chamber. I have seen as many as four sense organs in the course of a single ampullar canal.

UTRICULUS.

The utriculo-sacculus of the Hagfish (Pl. IX, Fig. 2 and Cut 2) includes all the body of the internal ear, exclusive of the relatively large ampullæ (*a.* and *a.p.*), and represents the little modified remnant of the auditory vesicle after the production of the two ampullar organs and their confluent canals (*c.a.* and *c.p.*). The utriculo-saccular sense organ (the maculæ acusticæ utriculi and sacculi) covers a considerable portion of the floor of this chamber, and is drawn out into an oval band ; its division into discreet sense organs is at least indicated by the manner in which the nerve branches are distributed to it. The walls of the chamber, especially in the region of the nerve entrance, on its ventral face, show the beginnings of the groove which becomes so prominent in the Petromyzon ear, caused by a meridianal constriction of its wall corresponding to the internal perforated partition. This partition in Myxine does not separate the sense organ into two parts.

Petromyzon (Pl. IX, Fig. 2 ; Pl. X, Fig. 2).

The Lamprey has developed along the line marked out in Myxine, and as a result the utriculo-saccular cavity is well separated into two distinct chambers communicating by means of the large sub-central perforation of the membranous partition. The partition is incomplete above, where the semicircular canals open into a common chamber, and below, where their ampullæ open out onto its floor. This partition has been described as a pair of folds, one of which occupies the inner face of the external wall of the ear, and the other of which occupies the inner face of the medial or inner wall. The position of both of these vertical folds is indicated on the exterior by grooves, that of the outer fold being the deepest and serving to mark off very distinctly the anterior chamber or the utriculus from the posterior chamber or the sacculus.

As the folds approach the bottom of the chamber, they become lower and indistinct. The floor of the chamber adjacent to the middle of the posterior wall is depressed, or pushed downwards, inwards, and backwards, forming what I shall designate the lagena. This pocket lies entirely within the territory of the sacculus, although the anterior third of it appears to com-

municate directly with the utriculus, while the posterior two-thirds communicate with the sacculus. The walls of this evagination do not show a continuation of the utriculo-saccular partition, as Ketel (160, 1872) and Retzius (237, 1881) have maintained and as it appears at first glance, for a careful study of the partition shows that it exists on the floor of the ear as a low fold, and that it is pushed cephalad by the lagena to such an extent as to mask the true position of this chamber. The recessus utriculi lies cephalad of the partition and forms a depression in the floor of the utriculus.

The canals, their ampullæ trifidæ, and the endolymphatic ducts offer exceptional features; but as I shall describe them more fully in another paper, they need not detain us here. The sense organs included in the Petromyzon ear are seven in number: the maculæ utriculi and sacculi, each discreet sensory patches, the cristæ acusticæ ampullarum anteriores et posteriores, also discreet, and the papilla lagenæ, which is possibly continuous with the macula utriculi, the sense organ in the recessus utriculi, and the sense organ of the undeveloped external ampulla, about which we need more information.

Beginning with the macula utriculi anteriorly, we find this sense organ placed anterior to the plane of the utriculo-saccular partition. It passes over the anterior edge of the sacculo-lagenar pocket, down its anterior wall, and out over its floor for a short distance. It does not reach to the base of the hill which lies in the bottom of the saccular portion of the pocket (*i.e.* the lagena). Its epithelium passes out into the columnar lining of the pocket, and this, in its turn, soon increases in height and becomes columnar as it ascends the hill, or papilla lagenæ. The epithelium on the posterior face of the papilla does not change again, but is continuous, with at most only an indication of a break, with the macula sacculi.

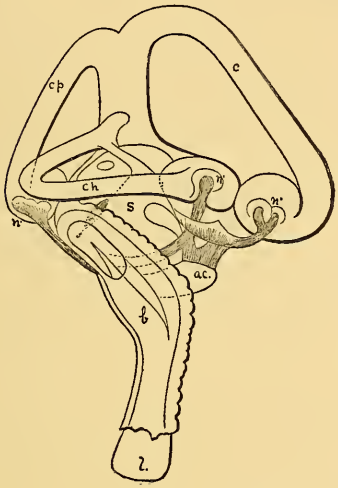
Mimus polyglottus (compare Cut 10).

The utriculus of the Mocking-bird is relatively very small, and is somewhat tubular, that portion of it containing the macula utriculi being marked off from the more central portion by a constriction of the walls of this chamber, followed by an enlargement, the chamber of the recessus utriculi, which is somewhat flattened from above downwards. It has a reniform

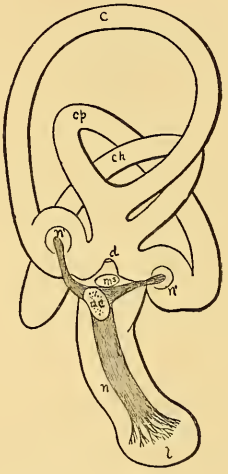
outline seen from above, but is decidedly oval seen from the side. The concave floor (from within) supports the macula utriculi and is carried over into the mouths of the ampullæ of the anterior and horizontal canals. The macula utriculi covers most of the floor and is irregularly oval, being very much larger at one end than at the other. The sensory hairs are very long and support a layer of otolithic bodies.

Alligator (Cut 9).

The utriculus in this reptile has assumed a tubular form, and, as compared with the enlarged sacculus, no longer appears as a



Cut 9. — The right internal ear of *Alligator mississippiensis*, seen from the outer face. Figure after G. Retzius. The figure outlines do not bring out the relations of the parts distinctly, and only the more important parts are lettered. *ac*, auditory nerve; *b*, pars basilaris cochleæ auct.; *c*, anterior canal; *ch*, external canal; *cp*, posterior canal; *l*, lagena; *n'*, cristæ acusticæ of the ampullæ; *s*, sacculus.

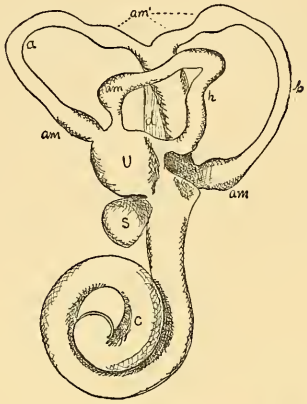


Cut 10. — The right internal ear of *Turdus musica*, seen from the inner or neural face. Figure after G. Retzius. The letters are placed only on those parts of the organ plainly visible in the figure. *ac*, acoustic nerve; *c*, anterior canal; *ch*, external canal; *cp*, posterior canal; *d*, ductus endolymphaticus; *l*, lagena; *ms*, macula sacculi; *n*, lagenar nerve; *n'* cristæ acusticæ of the ampullæ.

chamber of equal value, structurally and functionally, with the latter.

Man (Cut 11).

In Man and other mammalia the utriculus[1] forms a small chamber, from which are given off seven processes. Five of these belong to the canals; the other two are the canalis reuniens and the utricular blind sac. The utriculus and sacculus, although nearly equal in size, are very small relative to the long, enlarged cochlea, and they are relatively of less importance than in the Alligator.



Cut 11. — The left internal ear of a human embryo, 22 mm. in length, seen from without and below. Figure after W. His, Jr. The figure is from a model constructed from serial sections, and represents the ear much magnified. *a*, anterior canal; *am*, ampulla; *am'*, amæ (the middle reference line is superfluous); *c*, cochlea; *d*, ductus endolymphaticus; *h*, external canal; *s*, sacculus (in the restricted sense; really only the recessus sacculi); *u*, utriculus.

SACCULUS.

The saccular region of the Torpedo, viewed from the side, is a somewhat sickle-shaped body, with the cutting edge of the sickle blade directed forwards, downwards, outwards. The sacculus proper is a broadly rounded sac with scarcely a constriction where it opens into the common utriculo-saccular chamber above. The long axis of the sac bends backwards and outwards from the axis of the common chamber of the ear, while its lagenar prolongation carries the axis forwards by a bend at the point of origin from the sacculus. The sacculus possesses one of the canal sense organs, and its lagenar prolongation contains a bud from this organ which in the higher forms grows out into and forms the major portion of the cochlear organ. The utriculo-saccular chamber of other vertebrates, as of the forms described above, is really the transformed canal of the primitive auditory organ, some of the offspring remaining in the parental canal with parent organs just as the macula abortiva

[1] It should not be forgotten that the utriculus of these forms is really the primitive utriculus plus a small portion of the primitive sacculus, *i.e.* that part of the chamber from which the posterior canal arises is of saccular origin.

and the crista acustica posterior do in the case of the posterior canal.

Among the forms occurring between the Elasmobranchs and the Mammalia we find almost every conceivable gradation between the simple sacculus of the Cyclostomes and lower Elasmobranch species and the very complicated and highly differentiated structure known in the Mammalia as the cochlea and its organ of Corti.

The Hagfish can be said to possess a sacculus in its simplest condition in the first stages of development. The auditory chamber, designated sacculus by Retzius, is clearly the utriculo-sacculus of other forms. The separation being indicated by the very meagre transverse furrow in the bottom of the basal or ventral portion of the ear sac, and by the branches of the auditory nerve distributed to the compound sense organ, which covers more or less completely the floor of the double chamber.

Petromyzon presents us with an advance on the Myxine condition, for here the median raphe has acquired a greater size, but the anterior and posterior halves of the chamber are still in open communication with each other. They have, however, developed pocket-like processes, which represent the first traces of the recessus utriculi and of the legena of the higher forms.

Alligator.

In this reptile the sacculus has become distinctly marked off from the utriculus, and is only connected by a much reduced canalis sacculo-utricularis. The avian sacculus communicates even less freely than the reptilian, though within the group there is a constant reduction of the connecting canals progressing from the lower to the higher types. In other particulars there is no essential difference between the saccular regions of the two groups.

The sacculus of the Mocking-bird is a minute chamber placed alongside the utriculus, with which it communicates by means of an opening, all there is to represent the longer canalis utriculo-sacculus, so well developed in some of the lower vertebrates, and by means of the canalis sacculo-cochlearis it opens out into the cochlear tube. This canal is a long, curved tube of relatively large dimensions, and is formed by the secondary constriction of the neck of the cochlea.

In the Mammalia at last we find the two chambers in the adult entirely separated so far as the sacculo-utricular canal is concerned. The two chambers are connected indirectly by the splitting of the ductus endolymphaticus, whose proximal portion is involved in the division of the ear chamber and really represents the utriculo-cochlear canal. It should be emphasized that the division of the internal ear is not into upper and lower portions, so far as the primitive auditory vesicle and its sense organs are concerned, but into anterior and posterior portions, the latter of which very soon assumes a ventral position, which is constantly magnified and increased ever after during the development of the phylum. It is very important to keep this distinction in mind when trying to unravel complications of structure of the mammalian ear which were puzzling enough to gain the name of auditory labyrinth.

LAGENA (COCHLEA).

The lagenar tube of the Torpedo is a short, curved, blind pouch given off from the sacculus. It forms a continuation of this chamber downwards, backwards, and outwards. The evagination is developed from the floor of the chamber, but owing to secondary changes involved in the separation of the lagenar papilla from the saccular or parent sense organ, the pocket many times appears to be an evagination of the lateral walls of the chamber. In the Sting Ray such is the case (Fig. 1), while in the ear of Carcharias (Fig. 3) the lagena is a quite shallow depression in the floor of the sacculus near its posterior wall. A cochlea in the restricted sense of the term has not yet made its appearance.

As already stated, Myxine shows no trace of a lagenar pocket, but Petromyzon has acquired a distinct chamber and sense organ in the manner described, which are homologous with the parts of the lagena in the Elasmobranchs.

The position occupied by the lagenar opening in the wall of the sacculus in the Petromyxon ear is a peculiarity of the group. The lagena appears to open upward into the common utriculo-saccular chamber, its opening passing through the plane of the utriculo-saccular partition. On the completion of this partition, which is scarcely indicated in Myxine, but which is well grown

in Petromyzon, the ear chambers would communicate only by the separated ends of the endolymphatic ducts (Pl. IX, Fig. 2), as in the Gnathostome type, and, as will be perfectly evident on the inspection of the diagram mentioned (which, although a diagram, is true to the anatomical relations of the parts in Petromyzon), that the lagenar sack would be divided into two chambers entirely cut off from each other, the anterior or the utricular being the smaller of the two and containing a portion of the macula utriculi, the posterior and (two times) larger containing the well-formed papilla lagenæ and a part of the macula sacculi, which laps down over the edge of the pocket. These two pockets would thus communicate with the posterior inner and anterior inner angles of the utriculus and sacculus respectively. I was at first inclined to think that the cochlear and utricular recesses had been formed in this manner, but the discovery that the utriculo-saccular partition was continued cephalad of the lagena, and further, that there exists in the Petromyzon ear an independent utricular recess, decide the question as to the value of the Cyclostome lagena. It is purely a saccular pocket.

In the higher forms the lagenar pocket appears to be given off from the posterior outer angle of the sacculus, and has thus been displaced backwards and outwards.

In the bony fishes the lagena offers nothing of unusual interest for consideration here, and it is not until we reach the higher ichthyopsoid forms that the papilla basilaris, the parent organ of all the genuine cochlear structures, is developed. It is first produced, so far as our knowledge of living forms reaches, in the Anura, among which and the lower Reptilia it remains undeveloped and probably functionally insignificant. When, however, we reach the Saurians, the organ undergoes great changes in its structure, and in the Crocodilia reaches a condition of development but little if at all inferior to the Monotreme cochlea.

Alligator (Pl. VII, Figs. 2, 4, 7, and 9; Pl. X, Figs. 3 and 4).

The cochlea of the Alligator forms a depressed tube of angular outline and of relatively large size. It is curved in two directions, but not in as marked a degree as in Mammals and some Birds, though it approaches the Monotreme condition in this

one thing and has as great a curvature as some species of Birds. The importance of this spiral twisting is due to the fact that the Alligator belongs to a group of animals possessing all grades of development of the cochlear pocket or tube, as the case may be. The lower members of the reptilian class have a lagenar pocket not much advanced beyond the Torpedo condition, while the highest families of the class show a greater differentiation of the cochlear tube with its contained organs than the Birds. Thus in the Saurians the cochlear tube begins a spiral twisting that is carried on through the whole of the mammalian group. The homologies of the cochlear framework I cannot enter into in this place. The roof of the cochlear tube acquires such relations to the bounding walls and is so sharply marked off from the side walls in some parts as to form a membrana Reissneri with nearly mammalian characteristics.

The membrana basilaris is composed of three superposed layers of fine, parallel fibres, packed closely together in the form of three continuous sheets, of which the middle one is the best developed. The membrane itself is not pierced by the cochlear nerve as in Mammals, for the nerve enters the membrane after piercing the cartilaginous frame of the inner edge, and is then distributed to the different parts of the cochlear organ by radiation to the inside and outside from a point in the floor near the middle of the sensory structures. In its thickest parts the membrana basilaris is thicker than the remaining parts of the cochlear organ, and is suited in nowise as a vibrating membrane (Pl. X, Fig. 3). The fibres of the middle layer cross from one side to the other of the framework, and in the thickest parts of the membrane present a very characteristic appearance, as indicated in Pl. VII, Fig. 2; and Pl. X, Fig. 3.

Retzius thought that only the middle epithelial ridge of the cochlea was concerned in the auditory function as a nerve-end organ. This he called without hesitation the papilla acustica basilaris, and considered it to be the homologue of the organ of Corti. In this, however, he is in error. Besides the very important organ he recognized, there is another, nearly as large, lying to the inner side of the incipient organ of Corti, which Retzius has several times imperfectly figured. He has likewise correctly given the relation of the membrana tectoria to it, as seen in ordinary preparations of the Alligator ear. This other

organ, which I shall call the Sauropsid organ, lies upon the inner cartilage, and bears the same relation to the first named organ, which I believe to be the incipient organ of Corti, that the large epithelial ridge does to the small epithelial ridge in the developing mammalian ear.

The hair cells are more widely separated in these two organs of the Alligator than in the mammalian organ of Corti, and in consequence the membrana tectoria is looser in texture, but owing to the absence of otoliths and the strength and size of the individual hairs, the membrane appears much simpler in structure than that of the lagenar organ, for example. I have positive proof that there is nothing in the Alligator's membrana tectoria other than the long filaments into which it is with no great difficulty resolved, and there can be no doubt that these filaments are normally continuations of the auditory cells as their proper hairs.

Mimus polyglottus (Pl. VI, Figs. 6 and 8).

In the Mocking-bird the internal ear lies in the occipital face of the skull. The anterior edge is presented outwards, the posterior inwards, and the outer face looks downwards and almost directly backwards.

The anterior canals lie in planes nearly transverse to the long axis of the body, instead of occupying positions very nearly parallel to the sagittal plane. They are not, however, perpendicular to the long axis. The posterior canals lie very close to the edges of the foramen magnum; in fact, may be said to take part in forming its thickened border. Owing to the curvature of the occipital face of the skull, the so-called horizontal canals lie very nearly in the vertical plane and transverse to the long axis of the body.

The sense organs found in this type of ear are —

1. Macula utriculi.
2. Macula sacculi.
3, 4. Cristæ acusticæ ampullarum (anterioris and horizontalis).
5. Crista acustica ampullæ posterioris.
6. Crista acustica abortiva.
7. Papilla acustica basilaris.
8. Papilla acustica lagenæ.

COCHLEA (LAGENA).

In this account of avian cochlea no mention is made of the scala vestibuli or tympani, but only of the endolymphatic tube, or cochlea proper, — scala media. The cochlea of the Mocking-bird is an elongated pocket hanging down from the floor of the sacculus. In length it equals more than half of the vertical height of the whole ear and approximates one-third its length. Its diameter in the adult is greater than that of the sacculus. Its course, referred to the planes of the body, is downwards, inwards, and backwards. Its general shape and the main anatomical features do not differ materially from those of the pigeon, as described by Hasse and Retzius.

The lagena is relatively larger and more sharply marked off from the basilar portion than it is in the pigeon, and the latter part is more distinctly triangular in shape, with its base joined to the sacculus by means of the narrow canalis sacculo-cochlearis.

The cochlear canal is doubly curved, *i.e.* it has the form of the basal part of the cochlear canal of the Mammal ear, but projects from the saccular region more nearly perpendicular to the vertical axis of the whole organ than does the cochlea in the latter group.

The first curve is a bend transverse to its long axis and affects the upper portion of the tube most ; the second curve is more equally distributed throughout the length of the tube. The upper two-thirds of the canal is occupied by the basilar sense organ, while the lower third is taken up by the constriction which marks off the lagenar pocket.

The lagenar pocket is nearly filled with the lagenar sense organ, the floor of the pocket, with the exception of a border all around, being covered by the sensory epithelium.

Already in the bird the pseudo-cartilaginous oval frame which supports the cochlear organs has made good progress toward forming a protective case for the whole cochlear apparatus. By the fusion of the lateral bars of the frame in the lower half of their course the scala tympani is inclosed with the cochlear duct. The fibres of the cochlear nerve enter the cartilage at once after leaving its ganglion in the form of a continuous sheet of threads, and passes through the edge of the basilar membrane to be distributed to the sensory cells on its vestibular surface.

Alligator (Pl. VII, Figs. 2, 4, 7, and 9; Pl. X, Figs. 3 and 4).

The sense organ of the basilar portion of the cochlea is composed of two groups of cells, or two epithelial ridges, which run nearly parallel with each other. There are other epithelial ridges which, however, do not seem to contain sensory cells (Fig. 3, *e.e.'*). The larger or middle ridge is the most prominent part of the organ, and is the homologue of the small epithelial ridge of the Mammal ear; the inner ridge (*l.e.r.*) is the homologue of the larger epithelial ridge of the Mammal embryo and bears, especially on its outer border, hair cells similar to those covering most of the smaller epithelial ridge; but whether its entire surface bears cells auditory in function remains to be determined.

The middle region of this ridge has near its inner border several rows of large hair cells, which vary in number with the place from which the section is taken. At the extreme ends no cells are seen, yet on advancing toward the middle of the ridge the hair cells appear, first as a single row, then double, triple, quadruple, quintuple, and on up to eight neighboring cell rows near the middle of the papilla.

These very remarkable cells are the large hair cells and occupy the inner border, while the remainder of the papilla is made up, or, more correctly, covered over with the smaller hair cells. But above and below the middle of the papilla the rows number eight to ten, while in the middle part of the sensory patch there are found as many as twenty cells in transverse section.

The sensory epithelium is supported by a lamina reticularis, which rapidly fades away towards the sides. As one nears the large hair cells the meshes become incomplete. This reticular membrane is especially pronounced in osmic preparations, scarcely visible in Müller preparations, and here as elsewhere it is an artifact.

The supporting cells are long and irregularly cylindrical cells, which reach from the surface of the basilar papilla quite to the basilar membrane upon which they are inserted. They bear their nuclei in the basal portions of their cell bodies. They are loosely placed, with considerable interspaces between the cells.

Retzius concluded that neither representatives nor develop-

mental stages of such representatives of Corti's arches are present in the Alligator, and my own studies are only confirmatory of this view.

The nerve fibres pass from the cochlear ganglion as medullated fibres through the holes of the zona perforata, lose their sheaths, and ascend in the basilar papilla, spreading out fan-shaped in the transverse axis, from the point of entrance and end in the bases of the hair cells.

Mimus polyglottus (Pl. VI, Figs. 4, 6, 7, 9, and 10; Pl. VII, Figs. 1–9 and 12).

The sense organ of the basilar portion of the cochlea lies upon the basilar membrane as a two (several) layered plate of cells, broadest in its upper portion, gradually narrowing downwards, like the basilar membrane. It is rounded off at both ends. The sense organ occupies only about two-thirds the breadth of the basilar membrane, but *is not confined to this membrane.* It rests upon the quadrangular cartilaginous frame of the basilar papilla up to the entrance of the nerve fibres into the organ, or, in terms of mammalian anatomy, the habenula perforata. It is separated from the lagenar sense organ by an interval free of sensory epithelial cells. These two sense organs, though originating by the division of the primitive cochlear sense organ, are in the bird distinctly separated, and their nerves show even more distinctly the separation of the two structures.

In cross-section of the papilla basilaris the epithelial cells are largest near the inner border, but gradually increase from both sides towards the centre. The highest cells are, however, placed nearly over the edge of the cartilaginous frame. Between the middle and the inner border of the outer third of the basilar membrane the sensory epithelium passes into the ordinary lining of the cochlear canal. The number of cells in transverse rows in the broadest part of the membrane, *i.e.* near the middle of its length, is about forty. The cells are much shorter than in the other sense organs, and they are well isolated by the supporting cells. The cell caps are quite regularly hexagonal. Two important features of difference between the Thrush and Alligator cochlea are the absence in the former of the epithelial ridges found in the alligator and the absence of the large hair cells.

The cochlear organ thus appears to be made up of a large number of similar hair cells in the form of an even plate.

Although both Retzius and Hasse conclude that in the papilla basilaris of the bird we do not have a genuine organ of Corti, they consider the membrana tectoria of this organ as the homologue of the membrana Cortii of the mammalian ear.

Retzius describes this membrane as a somewhat soft, homogeneous, gelatinous skin, whose substance is perforated with many holes. In cross-section triangular, it varies in different parts of the organ, both in size and shape. He figures (Pl. XVIII, Fig. 13) two very distinct parts, which he describes as having somewhat different structures. That part (*mts.*) which lies against the clear cylinder cells of the inner border of the organ has its long axis placed perpendicularly with the basilar membrane, while the larger part (*mt.*), or the membrana tectoria propria, always lies with its long axis (in cross-section) placed parallel with the surface of the basilar papilla, as is readily seen from his figures. The tectorial membrane lies somewhat above the surface of the sensory cells, so that a narrow cleft is left between them, into which (across which) the hairs project. The membrane does not extend to the inner border of the papilla, and consequently three or four rows of the inner hair cells are left uncovered. The other hairs come in contact with the surface of the membrane, and in many cases seem to project into the holes of the membrane. These inner hairs Retzius found covered by the peculiar long hyaline cells. The membrane reaches quite to the outer border of the sense organ. As the nature of the tectorial membranes will be discussed in another chapter, it will suffice to say here that Retzius did not observe the tectorial membrane in its living condition and normal relations.

The tectorial membrane of the lagenar organ is apparently composed of the irregular network of fibres inclosing numerous otolith crystals, especially in its upper part. The otoliths lie either on the surface of the network or partly imbedded in it. Such is the appearance of the membrane as a whole in ordinary preparations of the ear.

Alligator (Pl. X, Figs. 3 and 4).

The sense organ of the lagenar portion of the cochlea rises gradually from the lining epithel of the lagenar chamber. It

is completely separated from the basilar papilla, and lies entirely below and beyond it in the cochlear canal. It covers more than a zone of the floor of the lagena, and reaches up on the side walls of the chamber. The outer (*i.e.* anterior) end even passes over on to the roof of the pocket.

In structure the papilla lagenæ resembles the macula sacculi.

Mimus polyglottus.

The sense organ of the lagena forms a somewhat horseshoe-shaped structure, which occupies the central part of the floor of the lagena. Its boundaries are rendered conspicuous by the presence of a sharply defined, white otolithic mass which adheres to the tips of the long hairs of the sensory cells. The rest of the floor is covered by a single-layered epithelium composed of regular polygonal cells. The papilla lagenæ has its long axis transverse to the vertical (primary) axis of the lagena, and is one and one-half times as long as the lagenar pocket is broad. The sense organ consequently curves up on to the sides of the pocket and reaches for a short distance on to the roof portion of the pocket (not the membrana Reissneri).

The histological characteristics of the sensory and supporting cells of the sense organs are essentially the same as have been already given for fishes. The cells connected with the nerve fibres are quite uniformly flask-shaped and in general bear much longer hairs than the authors have figured or described.

According to Retzius, the auditory hairs are tolerably stiff, straight, fibrillate, conical structures, which rise from a well-defined cuticular plate as a base. This plate forms the cap of the sensory cell. His measurements of the hairs gave lengths varying between 0.048 and 0.005 mm. They end finely pointed, the point being frequently turned to one side. Retzius leaves the question of the nerve terminations in the sensory cells in part an open question. He describes and figures one mode of termination as certain. In preparations of the cristæ acusticæ (maceration preparations) he found the thicker nerve fibres ending in expanded plates in contact with the bases of the sensory cells, and believes that the cell protoplasm here fuses with the nerve axis cylinders. Other and finer fibres he found with unattached ends *between* the cells some distance above their bases.

My own studies lead me to look upon the nerve plates which

Retzius figures as products of the maceration process, perhaps of both reagents and manipulation, and I am confident that the nerve fibres which this author finds between the hair cells, or rather in situations such that he thinks they lay normally between the cells, do not have this relation to the living hair cells.

TECTORIAL MEMBRANES.

Alligator (Pl. IX, Figs. 3 and 4).

The membrana Cortii (tectoria) in fresh condition is a soft structure which is greatly contracted by alcohol, but is well preserved in dilute glycerine to which a trace of osmic has been added, after which reagent it appears striated from base to upper surface. It is clear as glass, and it is honeycombed by irregular canals in all its parts. It is applied to the whole of the surface of the basilar papilla. Its transection at any point resembles in shape the cupula terminalis of an ampullar organ. The lower surface of the membrane near the middle line shows the most and largest pores. In ordinary preparations the membrane appears to be fixed by its inner edge to the large epithelial ridge, and from here to extend freely out over the surface of the organ, roofing over the groove between the large and small epithelial ridges, but coming to an end before reaching the outermost hair cells.

The horseshoe-shaped membrana tectoria of the lagena is composed of a dendritic network of many homogeneous fibres. Masses of otoliths are inclosed in the meshes, especially in the upper part of the structure. Retzius describes it as a tolerably thin horseshoe-shaped otolithic mass, containing larger crystals than are found over any other sense organs.

In the sacculus the otolithic accumulation nearly fills the chamber without showing any specially well-developed membrana tectoria. Retzius failed to find the latter. The hairs are present, however, and lie close to the tops of the sensory cells.

Mimus.

In the Mocking-bird I have always found the hair plate of the cochlear organ in osmic acid preparations and always free of otoliths. Its structure is shown in Fig. 10, Pl. VII. The

meshes of the network are relatively wide, usually oval in shape, with the long axis of the oval parallel with the course of the auditory hairs, which in the membrane are glued together in bands separated incompletely by the interspaces. The membrana Cortii is characterized by radial striations, while the "membranes" over the maculæ utriculi and sacculi are more loosely put together, and appear to be made up of a network of fine fibres. These fibres anastomose freely and are structureless and hyaline under ordinary powers of the microscope. With requisite treatment and sufficiently high powers the meshes of the network are seen to be composed of bundles of fibrillæ. The otolithic crystals are supported on the upper surface of the tectorial membrane and are disposed in several layers. How they are retained in place is not apparent. The extreme edges of the membrane are free from the crystals.

OTOLITHS, OTOCONIE.

Otolithic calcareous matter is deposited in the ears of all vertebrate animals. It is precipitated out of the lymph at first in the form of small granules usually crystalline. These primary otoliths grow as all crystals grow when immersed in solutions containing their salts under proper chemical and physical conditions. The calcareous salts are supplied in two quite different ways. The first and probably the most important source in the adult ear is the lymph which, passing from the blood-vessels into the cavity of the internal ear, contains the calcareous salts in solution. The second and probably most important source of calcareous matter during embryonic life is the auditory epithelium which during its passage through the ontogenetic stages of its development exerts one of its phylogenetic functions, that of calcareous secretion, for dermal purposes. This embryonic activity gradually gives way as the adult functions of the cells become more and more pronounced.

The otoliths of the vertebrate ear are then by nature foreign bodies, just as renal and vesical calculi are, though of course there are certain differences in the conditions leading up to their production in the different organs. Those vertebrate forms which retain most of the primitive relations of the auditory organs deposit most calcareous matter (*e.g.* Sharks, Skates),

though it is occasionally true here that the otoliths are secondarily dissolved out by the sea-water: such dissolution is usually prevented by the plugging up of the entrance to the ear by a mass of calcareous matter imbedded in mucus.

The presence of otoliths over the area occupied by the maculæ utriculæ and sacculi in all vertebrates, and the assumed universal presence of these structures in the auditory organs of all invertebrates, has led P. Meyer into a speculation as to their significance. He starts with the assumption that Johannes Müller had *proved* that the otoliths in fishes were of service to the animal in audition by reinforcing sound by resonance, whereas this was merely a supposition of Müller's. Meyer also points out that the membrana tectoria of the cochlear papilla basilaris is free from the otolithic structures present in the other cochlear organ of the Sauropsids, the papilla lagenæ. The speculations offered by this author are simply repetitions of some of the views already offered, and with the exception of those referring to the otoliths themselves are treated of in another place. The functions of the otoliths are entirely unknown; but, for my own part, I consider them foreign bodies, which, if now of functional value to the vertebrate ear, have acquired that value, or rather have forced the sensory structures to which they adhere with great readiness and in large numbers, to accommodate themselves to their presence. It is possible that they now perform their functions with the aid of the otoliths, though it is difficult to see what possible service the otoliths can render the auditory percipient elements, and their presence can be shown to be detrimental to the action of the percipient elements, as they execute their function in their primal state. Hence I may say that, so far as the otoliths are concerned, I am not in possession at present of facts enough to deny that they may play a rôle in auditory physiology. It is true, however, that they are not primarily necessary structures, for they are absent from the canal sense organs. They are produced in the greatest relative and absolute abundance in the lower vertebrate forms, whose ears retain connection with the sea-water, and whose blood is surcharged with calcareous matter; *e.g.* sharks. In bony fishes the separate particles, which in sharks always remain discrete, are united together, forming the ear stones.

There are many instances of calculi formed in other parts of the body, *e.g.* renal calculi, vesical calculi, pineal calculi, etc. These calcareous concretions or crystals lie within the normal cavities of these structures, or else within lymph spaces in their walls; they are abnormal, notwithstanding which they may exist for long periods of time within these organs without causing disturbance in the economy of the organ.

So far as my reading extends, the older observers have never put to themselves the question: Why do the otolithic crystals, which are heavier than the endolymph, occupy the surfaces of the hair cell areas, which as a rule project considerably above the surface of the floor of the auditory chamber in which they are found, and often in part lie on the side walls of the chambers of the ear?

Having greater specific gravity than the endolymph, the crystals might be supposed to be always dropping to a lower level until they reached the lowest, — the lagenar sac.

That this displacement of the otoliths could easily follow is a necessary consequence of the motions of the animal, giving gravity the opportunity to pull the crystals to the lowest level.

It is true that, generally speaking, the otolithic bodies occupy the lower chambers, but they do not necessarily, and do not usually lie in the lowest levels of these chambers, but defy the law of gravitation by remaining perched on the top of the hair cells or depending from the ends of the hair composing the hair field, as the case may be, according to the position of the sense organ on the walls of the chamber.

Most writers on the ear have contented themselves with saying that the sense organs were provided with a tectorial membrane (*Deckmembrane*), which frequently contained otoliths as integral parts. But as the tectorial membranes can now be conclusively shown to have no existence in nature as integral parts of the living sense organs, it remains to be explained how the otoliths are retained in place on the surface formed by the tips or the sides of the hairs.

One can hardly maintain that a mass of fine crystals of calcium carbonate weighing from one to two ounces, lying like a sediment upon the floor of the central chamber of the ear of a fish of six feet length (Blue Shark, *Carcharias cæruleus*), can really serve *any* physiological function auditory in nature, and I

have already shown that they did not *primitively* have such a function; and consequently, if they now have a function in the ear, it must be an acquired one.

We have no evidence that there is any special restraint placed upon the cells involuted with the sensory structures, — we will say in the Shark's ear, — and they certainly have not specialized in any direction, so far as we can see. All that they do is to serve as a lining of the auditory canal chambers, and the most that we are entitled to say, in the present state of our knowledge, is that they may have the function of secreting calcareous salts, held somewhat in abeyance, owing to the lack of external stimuli to encourage it.

While we are considering the question of stimulation, this fact should not be lost sight of; viz. during the time when the auditory sense organs were superficial in position the surface cells about them had this "*calcareous*" function in greater or less degree. It was controlled centrally, and carried out by alterations of blood supply. This control by inhibition or excitation was effected by a central co-ordinating mechanism composed of association fibres which brought into direct or indirect relation all the centres of the brain. Since these organs were superficial, their immediate surroundings must have been thus controlled; and since this control could only have been exercised through the fibres of the nerves supplying this region, it follows that the so-called auditory nerve must contain within it those fibres which controlled calcareous production on the surface; and since we are not at liberty to assume an entire annihilation of the co-ordinations of earlier days, it follows that there must be some sort of control of this function exerted on the lining cells of the auditory channels of the ears of all existing vertebrates, and that, when the function is exercised in local peripheral situations in response to local stimulation, it must be exercised by sympathetic action in the ear itself, and hence cause the deposit in the ear of calcareous matter, either amorphous or crystalline.

In this connection I wish to quote Hasse's observation on the nerve relations to the ciliate epithelium in Petromyzon. With reference to Ketel's researches on the Cyclostome ear, he says:

"Positive Beobachtungen für den Zusammenhang der Ner-

venfasern mit den Flimmerzellen hat er damals nicht beibringen können, allein es bleibt kaum eine andere Möglichkeit übrig und es sprechen dafür gerade die Beobachtungen Boll's [on Pterotrachea] und ferner der Umstand, dass bei Thieren, deren Schleimhaut auf ausgedehnten Strecken Flimmerepithel trägt, diese einen grossen Reichthum an Nerven besitzt. Ich zweifle nicht daran und ich hoffe, in Zukunft positiv beweisen zu können, dass, wo Flimmerzellen vorhanden, dieselben mit Nerven in Verbindung stehen, und wenn solche wie bei Evertebraten und bei Petromyzon in der Bahn der Gehörnerven verlaufen, so sind sie doch von ihm gesondert und als besondere Cerebralnerven anzusehen, die sich bei Petromyzon gleichsam zum Facialis gruppiren, und das Epithel ist nicht so ohne Weiteres als Gehörepithel aufzufassen."

As I have shown, the facial accessory nerve supplies sense organs in the ear of Petromyzon, and while I have no positive observations to record, it seems a more reasonable view to me that owing to the central relations of all peripheral nerves, which I have only faintly indicated in accounting for the presence of the otoliths, the ciliate epithelium is probably controlled by all the nerve branches entering the ear, *since it occurs in the chambers supplied by both anterior and posterior nerve branches.*

This view seems specially probable now that the main portion of the auditory accessorius is known to enter the endolymphatic and the commissural sense organs as *a sensory* nerve, leaving only a part of its fibres, on the most liberal allowance, to end in ciliate cells.

In tracing the otolithic bodies through the vertebrate phylum Hasse gives the following comparative account of their characters:—

"Wir finden bei Myxine glutinosa sowohl auf der macula als auf den cristæ acusticæ bröcklige Otolithenmassen, die jedoch bereits den cristæ der Neunangen, wie den Ampullen der übrigen Wirbelthiere fehlten. Bei ihnen finden wir die Otolithen nur an der macula recessus utriculi, sacculi, und cochleæ und zwar in derselben Weise, als zusammenhängende Kalkmasse, bei den Teleostiern, während wir dagegen bei den Plagiostomen Anhäufungen von einzelnen Kalkkrystallchen, Otolithenmassen finden. Solche finden wir auch bei den Amphibien im recessus

utriculi, im sacculus und im Endtheile der Schnecke, der lagena, die ja das Homologon der Schnecke der Fische ist, allein bei Siredon, Triton und Salamandra gestellt sich eine solche auch für den Anfangstheil der Schnecke hinzu, die aber bei den Ranæ wieder verschwunden. Von diesen Thieren an bis zu den Säugern finden wir dann nur Otolithenmassen im recessus utriculi, im sacculus und im Schneckenende, der lagena, dem häutigen Kuppelblindsacke und in dem letzteren des Menschen und der Säuger finde ich auch davon keine Spur, so dass bei ihnen die ganze Schnecke frei von Kalkkrystallen ist. Dabei finden wir dann immer und überall, das die Otolithen oder Otolithenmassen, und das gilt namentlich für sacculus, den Binnenraum desselben nahezu auszufüllen, so das nur geringe Flüssigkeitsmassen (Endolymphe) zwischen ihnen und der Sackwandung bleiben. Im recessus utriculi und in der lagena ist das viel weniger der Fall. Die Otolithen ruhen dabei immer den maculæ und deren Umgebung auf und werden selbst wenn sie aufrecht stehen, daran festgehalten und zwar dadurch, dass sie sich auf die immer gekrümmte Unterwand, den Boden, respective auf die Aussenwand stützen."

In criticising Hasse's views it should be borne in mind that he considered the terminal cupola of the cochlear spire to be a remnant of the lagena of other forms. He believed its sense organ had disappeared, and along with it the otoliths. The question of the homology of the apical portion of the cochlea cannot be considered as finally settled; but, leaving this aside, there is no question as to the fact of the disappearance; and this being the case, it is important to determine, if possible, the causes of the disappearance of the otoliths from this part of the ear. As yet the matter has not been investigated thoroughly enough to disclose a solution, though the idea that this phenomenon is directly connected with the increased delicacy of the cochlea at once suggests itself.

THE PERILYMPHATIC SPACES OF THE EAR.

These spaces are developed from the lymphatic spaces which are usually found well developed around the bases of the sense organs of the lateral line. These spaces have been described by Carrière, the brothers Sarassin, and others, and it is sufficient

here to recall the fact of their very general occurrence. Of the causes which have led to their enormous development in fishes, amphibia, and reptiles, with their reduction among birds and mammals, we know nothing definite. The physico-physiological conditions and consequences of this development I have not investigated.

CONTINUITY OF CEREBRAL AND AUDITORY SPACES.

According to Schwalbe, the subdural space in Man communicates with the perilymphatic spaces through the porus acusticus, and Key and Retzius found that not only the subdural, but also the subarachnoidal space was accessible through the perilymphatic channels.

Weber-Liel has shown experimentally that the perilymphatic spaces of the ear are connected with the subarachnoidal spaces about the brain.

The perilymph, according to Hasse, flows principally through a membranous canal, ductus perilymphaticus, through the foramen jugulare into the lymph channels at the base of the head,—some part of it passes in through the porus acusticus internus into the subdural spaces about the brain. The endolymph flows out through the arachnoidal sheath of the auditory nerve into the subarachnoidal spaces, and renews itself perhaps by transfusion through the ductus and saccus endolymphaticus. The continuity of these spaces is much more distinct in the fishes than in the higher forms.

COCHLEAR ORGANS OF THE MAMMALIA.

Pl. III, Figs. 1 and 2; Pl. V, Fig. 9; Pl. VI, 1; Pl. X, Figs. 3 and 4; and Pl. XII.

The Sauropsid organ.

Corti's organ in the Mammalia.

a. Relation of component structures and of the cellular elements. The cochlear frame.

b. Canal organ arrangement of the cell groups and the composition of a group.

c. The inner and outer hair cells.

d. The supporting cells. Pillars of Corti.

e. The hair band or membrana tectoria and the mb. reticularis.

f. The basilar membrane.
g. The cochlear nerves and nerve ends.
h. Marsupials and Monotremes.

The Cochlea.

Alle physiologischen Individuen, gleichviel welche morphologische Individualitäts-Ordnung ihr materialles Substrat bildet, sind in allen ihren Leistungen und Form-Verhältnissen auf die morphologischen Individuen erster Ordnung, die Plastiden (Cytoden oder Zellen) als "Elementar-Organismen" zurückzuführen, da jedes Bion entweder selbst eine einfache Plastide (Monoplastis) oder ein Aggregat (Synusie, Colenie, Complex) von mehreren Plastiden ist (Polyplastis). — HAECKEL, Generelle Morphologie, I, p. 370.

Der Organismus ist um so vollkommener, je abhängiger die gleichartigen Individualitäten, welche ihn zusammensetzen, von einander und vom ganzen sind, und je mehr also der ganze Organismus centralisirt ist, und alle subordinirten Individualitäten herrscht (Gesetz der Centralization). — *Ibid.* 372.

Der Organismus ist um so vollkommener, je höher zwischen allen untergeordneten Individualitäten welche ihn zusammensetzen, der Grad der Arbeitstheilung und der Grad der Wechselwirkung ist, je grösser mithin die Differenzirung und die Centralization des ganzen Organismus ist. — *Ibid.*

The general features of the development of the organ of Corti I have already given in the account of the morphology of the sauropsid and mammalian cochlear organs. In the following account which, though by no means exhaustive, will serve to illustrate the ontogeny of the organ, I shall dwell almost entirely on the organ of Corti proper, and shall have very little to say of the other parts of the cochlear apparatus; *e.g.* the scalæ of the cochlear walls except so far as they take part in the formation of the organ of Corti, or influence the performance of its function. The account is mainly based on my studies of the development as it occurs in the pig, although many facts have been verified for the rabbit, sheep, ox, opossum, and other mammals.

So far as my observations go, and they agree with Boettcher's, there are but the slightest differences noticeable in the development of the ear among the domestic mammals, the only ones heretofore studied with a sufficient degree of completeness for the purpose of comparison.

The first thing of fundamental importance to be noted is that the cochlear tube is accompanied on its sense-organ wall or floor by a ganglionic nerve trunk (*n. cochleæ*), an artery (*a. basilaris cochleæ*) of which the vascula spiralis is one branch, a vein (*v. basilaris cochleæ*), and a lymphatic canal of large proportions;

and since such structures accompany in an entirely similar manner the sense-organ canals in fishes, we discover in this new evidence of the nature of the cochlear tube.

As is well known, the cochlear ganglion arises in contact with the cochlear tube, and no sharp line of demarcation is at first to be seen between the sensory epithelium and the ganglionic tissue. This condition does not last long; for as the tube increases its size it becomes sharply marked off from the ganglion and before long separated from it, mainly, as it would seem, by the ingrowth of the intracapsular connective tissue, which at this time is beginning to assume its cartilaginous nature. The separation increases with the growth of the parts, until finally in the adult the sense organs in the cochlear tube are connected with the cochlear ganglion by a very long, narrow band of nerve fibres, as viewed in section transverse to the long axis of the canal.

The nerves pierce the floor (basilar membrane) about the line of contact of the small and large epithelial ridges.

The organ of Corti is the final product of a long series of developmental changes in the cochlear organ. The earliest condition of the cochlear organ in the mammal, which in its development very completely epitomizes the phylogenetic history, is of course the simple pocket budded off from the sacculus, its inner surface being lined with a columnar epithelium. To confine our attention to the points of most interest to us, we will pass over all the changes between this earliest condition and the stage in which the floor of the cochlear tube, now well grown out, has become thickened, the thickening being in the form of a ridge (later ridges) running parallel to the long axis of the tube. Kölliker, Middendorp, and Boettcher have described these elevations and applied to the two most prominent ones, which play the greatest part in the subsequent history of the mammalian cochlea, the names small and large epithelial ridges. The large epithelial ridge lies nearest the lamina spiralis ossea, and consequently is nearest the nerve supply; the small epithelial ridge lies beyond it outside, and receives its nerve supply only after the nerves have been given off to or passed through the large epithelial ridge.

Owing to their subsequent history, I shall call the large epithelial ridge the Sauropsid cochlear organ and the small epithelial ridge the mammalian cochlear organ or the organ of Corti.

As soon as these two ridges are formed, they are separated by a shallow groove which really forms a part of the sulcus spiralis internus in the adult condition, but in this sense only. The Sauropsid sulcus (internus?), as I shall call this groove, separates the two ridges, and its deepest part lies over the boundary line between the two ridges. Now since the large ridge disappears during postembryonic development in all mammals yet studied, it follows that at least half of the Sauropsid sulcus is taken up in and forms a part of the space left vacant by the large epithelial ridge, which is the sulcus spiralis internus. For a long time, relatively, the two ridges grow but little, but suddenly they both receive an impetus and begin increasing in size, the period in their ontogeny having arrived when this phylogenetic impulse must be reproduced. The larger ridge grows most rapidly under this stimulus, and this may be due to the more direct connection with the nervous centres controlling the organ. From their first appearance there is to be seen over them, covering their apices, a delicate whitish sheet of substance, supposed by Kölliker and others to be a gelatinous excretion from the cells themselves, but which more careful examination of properly prepared material shows to be composed of a forest of small hairs growing out of the tops of the cells, which in this manner are shown to be hair-bearing sensory cells, since, as mentioned above, they are connected with the fibres of the cochlear nerve.

The large epithelial ridge grows in two ways: by increase in the height of the cells, and by increase in its breadth, due to the division of the cells. As the cells increase in size, the hairs grow longer and apparently more rapidly than the cells, for they finally surpass them in length. Having reached its complete development, the large epithelial ridge remains for a time unchanged and in this condition is known as the Organon Köllikeri, this name having been applied to it by Hensen in honor of its first describer, A. von Kölliker. Kölliker's account of this organ is by no means complete, since he failed to make out of the covering membrane or mass anything more than a nearly homogeneous mass of gelatinous substance, which he supposed was simply the increased exudation noticed by him in the earlier stages. The significance of this structure was far from his mind.

The little epithelial ridge grows more slowly, and at the time the large ridge has reached the height of its development, it is still in a very immature state, though the structures which serve to distinguish it and make it peculiarly a mammalian organ are marked out so definitely that no parts are added to the organ as it now exists. From this time on, it is evidently the organ of Corti, though about this homology there exists in the literature a great amount of confusion. Retzius correctly recognizes the ontogenetic relation of the adult organ of Corti to the small epithelial ridge, but he says the organ of Corti is the homologue of the macula acustica papillæ basilaris, which it never is. Even among the higher Sauropsida (saurians and birds) there is such a differentiation of parts as to necessitate our recognition of the fact that the sensory plate of the papilla acustica basilaris of these forms cannot be considered the homologue of the simpler plate in the lower forms. Likewise, when we pass by the unknown forms between the Sauropsida and the Mammalia we find ourselves face to face with an entirely new organ that has, at most, only the slightest indications of its beginnings in the ear of the Alligator, the intervening stages of development so far as at present known having been annihilated with their possessors, the Sauropsid ancestors of the Mammalia.

The causes which have led up to the annihilation of the large epithelial ridge during ontogenetic process as a part of the phylogenetic advancement of the Mammalia are very obscure as yet. For the present, suffice it to say that such is the fact, easy of observation, and that connected with this annihilation of the Sauropsid organ is the rapid advancement and perfection of the mammalian organ of Corti. The Sauropsid organ at the height of its development takes more of the nerve supply from the cochlear nerve than does the organ of Corti; but as the latter grows and the former fades, this condition is reversed, until the cochlear nerve gives off fibres to the organ of Corti alone. What becomes of the fibres supplied to the Sauropsid organ? Do they simply disappear through resorption? I have observed that the bundle gradually grows smaller, but I am unable to detail the process of disappearance.

The Sauropsid organ disappears through a process of resorption; that is, first of all, through a loss of its nutritive supply, and then by a gradual decrease in size of the cells until only a

few dwarfed remnants remain in the place of the once powerful organ of the Sauropsid type. The histology of the organ has already been given by Boettcher (31, 1869), Kölliker (166, 1861; 164, 1879), Retzius (237, 1884), and others, but only in a very incomplete manner. I am able to make some few additions to it, based on observations made on the organ in its mature state. The long cylindrical cells occupy the whole depth of the organ and fasten upon the developing membrana basilaris. They are polygonal columns, more or less bent, depending upon their position in the organ (Pl. VI, Fig. 1). Within, the protoplasm is clear and is provided with a single oval nucleus, which lies at different niveaux in different cells and in different parts of the organ. The cells are never multinucleate, as has been asserted by Boettcher (31, 1869). From the top of each cell there rises a long, slender hair structure, which curves over toward the inner edge of the organ over the region of the entrance of the cochlear nerve. This part of the floor of the cochlear canal is on a level (at this time) with the top of the cells of the Sauropsid organ, although the floor is here not near as thick as it is under (and including) the Sauropsid organ. In consequence, the hairs seem to fall over on to the surface of this plateau, the inner portion of which later on is known as the Limbus spiralis internus.

Owing also to the relation of this plateau, when the Sauropsid organ has disappeared the open canal occupied by the organ is left free, and over this the hairs of the organ of Corti project, roofing over the canal, but only incompletely closing it in.

The human *cochlea* may be taken as fairly representing mammalian conditions. It is not so much coiled as the cochlear tube of some of the higher Mammalia, but it stands much nearer the apex of the series than to the lowest members, as represented by Echidna and Ornithorhynchus, which are but little above the avian and saurian conditions. The human cochlear tube is a flattened canal having in different parts of its course a varying cross-section, from nearly circular and oval to distinctly triangular form. In the adult ear it possesses about three spiral turns, and along its floor, extending from one end to the other, is a linear series of sense organs so closely united together as to have been described as a single band-like sensory apparatus by all anatomists from its discoverer, Marchese Corti (1851), down

to the present time. Relative to the mass of the body, the longest cochlear tubes are found among the Chiroptera and the Rodentia, while the Cetacea possess the relatively smallest.

In the Mammalia the cochlear tube has become much more completely separated from the sacculus than in any other group of vertebrates. It is connected with the parent chamber by the narrow sacculo-cochlear canal, — the canalis reuniens of Hensen.

The term organ of Corti, as it is used in anatomy, is, strictly speaking, not sufficiently exact for scientific purposes, and some of the parts included in it have no functional relation to the physiologically active parts of the mammalian cochlear organ. Such parts as the auditory denticles and related structures have certainly no intimate relation to the working of the organ to-day, nor are they concerned in perfecting the organ structurally. They are simply the remnants of a previous condition of structure.

The mutual relations of the structures forming the organ of Corti vary in different periods of the growth and life of the organ. In the embryonic condition all the cells are firmly planted on the floor of the canal, and this floor is attached on both the inside and the outside edges to a thick cartilaginous plate or bar, the derivative of the parallel cartilaginous bars of the ancestral Sauropsids.

As all the cells are in contact with this basement or basilar membrane, which, although a thick plate at this time, thins out later to form a tensely drawn membranous structure, and as likewise all the cells take part in the formation of the free surface of the organ, they all have the same length, both supporting and sensory cells: indeed, it is extremely difficult at this early time to distinguish the supporting cells as such.

The first change of importance is marked by the appearance of the rods of Corti, by means of which the uniformity of the cell arrangement is broken up. The rods as they develop cause an elevation or upheaval of the two parts of the sensory plate, between which they have arisen, so that from this time on, in ever-increasing degree, till adult life is reached, the edges of the organ lying on the uplifting limbs of the arches are raised from the basilar membrane. The inner edge is disturbed the most, and the inner row of hair cells and some of the supporting cells no longer reach the basilar plate. The outer hair cells

almost always reach to the floor of the canal. The processes concerned in this uplifting cannot be detailed here further than to say that the bases of the rods of Corti spread apart while the apices remain united, and owing to the plough-shaped foot of each arch, they are readily forced under the neighboring cells. Working with this process, and perhaps more prominent than it, is the process of growth in the basilar membrane, by means of which the feet of the pillars are carried further apart. By the resorption of the Sauropsid organ and the growth in height of the whole organ of Corti, the latter comes to project from the basilar membrane into the cochlear canals, a long, well-rounded ridge, from the apex of which five to seven more or less complete[1] rows of hairs project in a sweeping curve over towards the foot of Reissner's membrane. As compared with the older conceptions of the structure of Corti's organ and the relations of its parts, the organ, as I have here briefly sketched it, is a simple and compact structure. There are many of the important histological intricacies yet to be made out concerning the cell parts and their relations to the parent and neighboring cells and to the nerves, but these need not detain us here.

The essentials of the organ of Corti are then, in brief, a long, fluid-filled canal, with a series of nerves piercing its floor to pass up among the cells of a ridge, the apex of which is crowned by several rows of long filamentous hairs which arise from the tops of the sensory cells with which the nerves connect.

The sensory cells are arranged in groups, but, as might be expected, these groups are by no means as regular as they would be were they free to multiply and shape themselves, as is the case of the sensory cell groups in the surface canals of fishes. It should be noted that after being shut up in the cranial box the canal organs were so hemmed in that there was no room to spare for the usual amount of canal space to accommodate a single sense organ, and the larger patches of sensory cells, such as the maculæ utriculi sacculi and the papilla lagenæ, were formed in a manner quite unlike the more typical cristæ of the ampullæ. With the lengthening of the lagenar pocket there was afforded opportunity for the growth of a series of closely related canal organs; the opportunity was seized; the sense organs grew in all directions, practically covering the floor of

[1] There are usually four quite complete rows with straggling cells beyond.

the chamber. These cells were, however, of low stage of differentiation, not raised above the cells of the maculæ sacculi and utriculi in physiological capabilities, and consequently the limit was soon gained for a useful multiplication of the sensory structures in this way. If a few cells could do all the work of the many and subserve other functions at the same time, it would be of advantage to the animal to reduce the number of cells, conserve its nerve energy, and gain in perfection of service.

Just this has been done in the transformation of the Sauropsid cochlear organs into the mammalian condition, but at the same time the length of the narrowed series has been greatly increased, so that information is reported to the brain from a hundred independent sources in the mammal ear where it was reported from ten in the Sauropsid ear, serially speaking; for the important condition of sequence is concerned only when the reporting cells are at different distances from the brain. Where all the cells are the same distance from the brain, they speak practically as one.

There is then a repetition of canal-organ arrangement in the cochlear organ of the Mammalia, and this is indicated by the nerve supply, the blood supply, the separation of the end cells themselves, and by all the subordinate structures that have been impressed with the structural relations of the sense organs and their connections. In Pl. XII, I have attempted to illustrate in a perspective view the existing condition of things in the human ear.

The structure of the hair-bearing cells in the cochlea of the mammalian ear has been a subject for difference of opinion ever since their discovery.

Waldeyer and Gottstein describe them as twin cells composed of upper and lower halves, the parts corresponding to the hair cells and the supporting cells of other authors. I have never found a double or twin cell among my many preparations, and I do not believe in their existence. The hair cells as I have found them correspond to the upper halves of the twin cells of Waldeyer and Gottstein, the hair cells of Retzius and of Paul Meyer.

The hair cells of the outer rows are larger than those of the inner. They are cylindrical in shape and filled with a clear fluid

in their upper parts, while their basal portions, around and below the nucleus, contain a coarsely granular protoplasm. There is not much variation in shape between the cells from the different mammals studied. In all species the basal end of the cylinder is quite regular, somewhat swollen, and the upper rim of the cell wall, where it joins the cell cap, turned out like a flange. This conformation gives the whole cell, when viewed from the side, a vase-like shape. The action of reagents on the cell contents affects their appearance, so that the clear upper half, so distinct in the living cell, may be coagulated or have its invisible structure more or less clearly brought to sight. Contrary to the statements of Retzius, the auditory hairs arise, as Waldeyer has already claimed, from the whole upper surface of the cell cap. The crescentic outline or horseshoe figure (hufeisen oder halbkreisförmiger Anordnung) or style of arrangement which Retzius has made us familiar with, is an optical effect and entirely illusory. The explanation of this mistake (which many other investigators besides Retzius have likewise made) lies in the fact of the oblique position of the hair-cell cap with respect to the focal plane of the observer's lenses, so that unless great care and a sufficiently high power is used, the apparent arrangement of the hairs in the optical section of the cell cap of the thickness of the focal depth is mistaken for the actual arrangement, which is usually only to be determined by a careful analysis and combination of the several images of the optical sections of any given cell cap. Whatever the shape of the cell cap, whether circular, oval, polygonal, or irregular, the hairs arise from the whole of the upper surface, and they are evenly distributed over this surface.

These hairs are more numerous on the hair cells from man's ear than the mammals which I have studied. The differences are not very great between man, the ox, and pig. Quantitative results I shall reserve for a later paper.

Retzius has shown conclusively enough that the human cochlea does not contain a larger number of rows of hair-bearing cells than that of most mammals, *e.g.* the dog and cat; but his calculations show the rows to be much longer in man than in the cat and rabbit.

The row of inner hair cells offers some important points for consideration, — points of difference in structure and perhaps

origin and development. These hair cells do not vary much in their characters in domestic animals. This row is the most complete of the several rows of the organ, and it shows supernumerary cells less often than the other rows. In histological details the cells are quite unlike those of the outer rows, and, according to Retzius, they approach those of the maculæ utriculi and sacculi in their shape, size, and structure. They are entirely filled with a dark, coarsely granular protoplasm, and consequently lack the clear end space of the cells of the outer rows. The hairs appear to be better developed than in the case of the cells of the maculæ.

According to Gottstein and Waldeyer, and Retzius agrees with them, the inner row of hair cells is developed from the outermost cell of the large epithelial ridge; but according to Boettcher the innermost cell of the small ridge gives rise to the inner hair cell. It becomes a matter of great importance for the correct understanding of the organ of Corti to determine the source of all its elements. For my own part I am fully persuaded that the inner row of hair cells arises entirely within the bounds of the small epithelial ridge, and the evidence is not merely embryological, as derived from the study of mammalian development, but comparative anatomical, based on the study of the organ of Corti in the Alligator and several mammalian ears. Allowing that the inner cell is developed from the outermost cell of the large epithelial ridge, we should have to separate the organ of Corti into two very distinct portions, one of which would include the portion supplied by the Sauropsid organ, *i.e.* the inner row of hair cells, and its supporting cells, or the inner row of Corti's pillars; while the other one would include the rows of the outer hair cells and the outer pillars of Corti. While my own observations on the ontogeny of the ear agree with Boettcher's, they are not sufficient to warrant at this time a final conclusion as to the part actually played by the Sauropsid organ in the adult mammalian ear. As I have said before, I think it disappears as a sense organ, being represented in the adult mammal only by the lining epithelium of the sulcus spiralis internus.

The structure of the Sauropsid and mammalian organs as they exist in the Alligator is such that I am inclined to think the whole of the organ of Corti as it exists in mammals is

a direct descendant of the organ of Corti as found in the Alligator, and for the following reasons: the Sauropsid organ of the Alligator is made up of sensory cells of a different character from those found in the Alligator's organ of Corti. This is especially true of the innermost four or five rows of the organ of Corti. For in these innermost rows the cells are more like those of the organ of Corti in the mammals than those of any other parts of the epithelial ridges, and are very different from the remaining cells of the organ lying outside of them.

I look upon these rows of modified cells in the Alligator's organ of Corti as the earliest indication of the peculiar and characteristic structures of the organ of Corti in the Mammalia; and if such is the truth, the latter organ must have arisen entirely from the former. Accepting the other supposition, we should necessarily have to conclude that the arches of Corti arose from the supporting cells of the edges of the Sauropsid and mammalian organs, and that Corti's canal is represented in the Alligator by the deep valley separating these two structures.

While it is entirely possible for the supporting arcade to have arisen in this way, and although such a method of origin would render some difficult problems much easier of solution, and has thus the factor of simplicity in its favor, it must be said that at the present time the latter view is not so well supported by facts as the former.

The arch of Corti in the mammalian ear (Pl. XII) is located outside of the place of entrance of the cochlear nerve into the cochlear canal, and in the Alligator the relation to the organ of Corti (*i.e.* the inner four or five rows of modified cells) is very similar, while the relation of the nerve to the Sauropsid organ is very different and of the same nature as that sustained by the cochlear nerve to the large epithelial ridge in the developing mammal.

The *supporting cells* of the organ of Corti, like those of all other sense organs of the lateral-line category, comprise all of the non-sensory cells of the ridge-like organ. So far as my observations enable me to decide, these cells are all simple, *i.e.* there are no twin cells in the sense in which Waldeyer, Gottstein, and Nuel use the term. Since the supporting cells, with the exception of the double row called Corti's pillars, are of

interest mainly from the histological standpoint, I shall not enter into a detailed account of them here. Suffice to say that they are of various sizes and shapes, depending upon their position in the sensory ridge, and they pass over into the indifferent epithelial lining, of the sulci internus and externus. The rods of Corti are of unusual interest, since they make their appearance among existing forms only in the Mammalia. In the Monotremes, where the cochlea retains a lagena, its main Sauropsid character, the arches of Corti are already well developed, and we must look for their early stages of growth and development among extinct forms of the *Post Reptilia*. The story of their development will be given further on; but when once matured they constitute the long tent-like cover or inclosure of the canal of Corti. Each rod is composed of a large number of isolable, fine, transparent threads, of circular section. The minute hyaline cylinders conform to the curvature of their rod. The whole bundle is inclosed in a cell which for the greater part of its length fits it closely like a sleeve, while at its foot and sometimes at its head the remaining protoplasm of the cell is collected. The cell nucleus, which persists throughout the life of the rod, lies always in the foot on the tunnel face of the rod. The fibres of the two rods opposite each other seem to blend at their union above, thus forming the keystone of the arch.

From here they diverge until they come in contact with the basilar membrane, when they turn suddenly outwards, *i.e.* away from the tunnel, and run parallel with the fibres of the basilar membrane, among which they sometimes appear to be rooted; and Nuel was led by this appearance to figure and describe a continuity of the pillar fibres with those of the basilar membrane. I am convinced such does not exist.

The cell caps of the cells forming the ridge of Corti are fused together,[1] thus forming a continuous sheet, and the pillar heads form a broad, smooth band, marked only by transverse and parallel lines, which, throughout the length of this plate, divide it into inner and outer halves, and these into segments (Pl. III, Figs. 1 and 7; Pl. IV, Fig. 6; Pl. V, Figs. 1[a] and 10;

[1] While in the living condition the caps of the epithelial cells are in close contact, in hardened preparations they are more or less soldered together by the action of the reagents, and their continuity is thus mechanical and not organic. They do not differ in this respect from other forms of epithelial cells.

Pl. VIII, Fig. 6; and Pl. XII). This plate, one part of which has received the name of Hensen's Randkörper, another part of which is known as the membrana reticularis, and whose third and inner part has never been specially named, will be considered more in detail further on.

The membrana basilaris is that part of the connective tissue wall of the cochlear tube which lies under the sense organ and forms its floor, as well as the basement membrane of its epithelium. Like the basement membrane of all sense organs of this system, it is a portion of the dermis of the head, modified in the direction of homogeneity of composition. Its structure and arrangement have been many times correctly described in detail, and I have little to add to its histology; but when we consider its morphological significance, I am sure that heretofore the true nature and relations of this now well-known plate have not been correctly apprehended. It is far from being the most delicate membrane of the cochlear wall, and is, as stated, actually the thickest part of the connective tissue wall which is exposed to the perilymphatic spaces. Reissner's membrane, or the roof of the canal, is very much thinner and less resistant, since its basement membrane is a very delicate plate and the two plates of epithelial cells covering it are many times more delicate than those supported by the cochlear floor. The membrana basilaris has only one character that renders it of special interest, and that is its relation as basement membrane to the sensory cells whose nerves must pierce it in order to reach their terminations.

Boettcher thought he had proved a structural continuity of the epithelium, *i.e.* the rods, with the basilar membrane, but from his embryological studies he concluded that the layers of the membrana basilaris were in no sense derived from the epithelial layer supported on its inner surface. This conclusion no one can refuse to acquiesce in when the evidence of comparative anatomy is considered. The epithelial cells of the sense organs of the lateral line are supported by the dermis on which they rest, which thus constitutes the basilar membranes of these organs. It normally develops lymphatic channels below the sense organs. Thus the dermis between the organ and the lymph spaces becomes the functional basilar membrane of the organ, and is very much thinner than the surrounding

dermis. These modifications do not affect the relation of the epithelial cells to the connective tissue cells, and the two layers retain their structural independence.

The basilar membrane of the organ of Corti is a complex structure composed of cells and fibres of varying sizes, which have arisen from the dermis. These fibres run both directly and obliquely across the open basilar space, and form a two to several layered floor, on which the cochlear organ rests. Anatomists have made various divisions of its surface, based usually on the relative position of the cochlear ridge and the nerve foramina to the surface of the plate. It is usually divided first into two main zones, an inner and an outer. The former is very sparsely striated, *i.e.* fibrous; for in this part the individuality of the fibres is more or less in abeyance. This part bears the organ of Corti, and runs under the sulcus spiralis internus, where it is perforated by the foramina for the nerves, to its insertion into the limbus spiralis.

The outer zone is usually considered to begin in the immediate neighborhood of the feet of the outer pillars of Corti, *i.e.* outside the arch of Corti, and extends from this region outward to its insertion in the angle of the ligamentum spiralis. The fibres of this zone are very distinctly separated from each other, and are easily separated in microscopic preparations of the membrane.

There are at least two layers of fibres present in this membrane in all mammals, and in some three and four. There is a general agreement among investigators that the basilar membrane of the human ear is thinner and relatively broader than it is in most, if not all, other mammalian species, a belief which I think is insufficiently borne out by the facts, but the number and completeness of the layers of fibres is subject to change during development, and is different for different species. The surface layers of both faces of the membrane are in the adult usually incomplete, and appear as bundles or bands of fine fibrils lying on the deeper layers of the membrane.

The basilar membrane in the pig and ox shows during its development that it is not in any way built up from the ecto-epithelial structures lying on its upper surface and derived from the surface of the head, nor from the meso-epithelial structures evolved during the ontogenetic processes as cellular lining of

the lymphatic canals of the ear, as was supposed by Deiters and Lavdowsky. The basilar membrane, considered phylogenetically, is merely a portion of the connective-tissue floor of the sense-organ canal of fishes.

Of the basilar membrane Retzius says (*loc. cit.* p. 280), "*Diese wichtige Membran, die Grundmembran des akustischen Apparates der Schenecke*, welche von Labium tympanicum bis zum Ligamentum spirale straff ausgespannt liegt, lässt sich am ehesten in die eigentliche Membran und die tympanale Belgschicht theilen." The lining tissue of the scali tympani or the lymph space normally developed below the floor of the sense organ is as normal a component of the basilar membrane as the cellular plate which covers the face of Reissner's membrane turned towards the scala vestibuli, and must be considered when we estimate the physical properties of the basilar membrane.

The importance of the basilar membrane to previous investigators was due mainly, if not entirely, to their views as to its function. It was the harp of many chords on which Helmholtz played with variations his later piano-string theory of musical perception. On Pl. VIII, Figs. 5 and 7 show the basilar membrane of the Opossum and its component layers, some of which are strictly transverse, while others run longitudinally, crossing the former nearly at right angles. These fibres are all held together as a compact plate during life, and are with difficulty separated enough to show their mutual relations. When hardened or properly macerated, they may be readily separated, and the upper layers are most readily displaced. These upper bundles of fibres have played an interesting part in the history of the mammalian cochlea, as will be further explained when we come to treat of the nerves. The histological character of this membrane has been so many times the subject of careful research that it might seem presumptuous for one to attempt to add anything to our knowledge of it. I do not intend to enter into any long account of the condition of the basilar membrane in the forms studied by me, but only to call attention to the facts (and illustrate them with a few camera drawings) that investigators have ascribed to the membrana basilaris qualities which it certainly does not possess. Its elasticity is not great enough to serve for the transmission of the

delicate undulations which it has been supposed to transmit, and from its composition a great deal of the motion imparted to it would necessarily be lost in transmission. Likewise before reaching the plate of transverse fibres which form the completest part of the basilar membrane as previously conceived, the motion would have to be transmitted through a continuous homogeneous layer of substance lying below and inclosing the fibres from the scala tympani.

When we reduce the cochlear spiral to a straight line, we have the cochlea in the form of a straight canal, receiving its nerves along one side — the lower inner angle, if one may speak of angles of a tube more or less oval in cross-section. The nerve does not enter the walls of the tube as a continuous band, but is previously divided into sub-equal sections, which form branches about twice as broad as thick. There are about fifty of these branches in the middle spiral of the ear of Sus and a total of from 110 to 125 in the entire cochlea.

Each branch of the cochlear nerve is supplied to a single sense organ composed of about ten hair cells counted lineally in either the row of inner hair cells or the inner row of outer hair cells. There is a tendency to fuse into a continuous band, owing to the suppression of the supporting cells between the sense organs, which renders the determination of the boundaries of most of the organs a matter of difficulty and in many cases an impossibility. Assuming that there are four rows of hair cells regularly completed, each fasiculus would supply on the average about forty hair-bearing elements of Corti's organ in the adult. The extremes I have found are four lineal and sixteen lineal with ten cells as the average length of the sense organ.

After passing through the floor of the canal the nerve fibres enter the epithelial ridge and traverse the intercellular spaces, branching, as they do so, until they arrive at the end cell, into which they enter. The general features of the relation of the nerve bundles, as they pass out of the lamina spiralis ossea through the habenula perforata, during the passage of which they lose their medullated sheaths, have often and accurately been described, and there is substantial agreement among the authorities in the matter, but the course of the non-medullated fibres from the habenula perforata to their ends, and the relation

they sustain to the other structure of the organ, are not so well agreed upon. The discussion which is at once opened when the subject of the peripheral endings of sensory nerves is touched upon is one of long standing and exceeding great difficulty when it comes to the presentation of demonstrations and conclusive arguments.

There are two questions remaining for consideration in this paragraph, — the spiral or longitudinal nerve bands and the peripheral ends of the radial nerves in the hair cells. Discovered by F. E. Schultze, described especially well by Deiters, the spiral nerves have been found by the majority of investigators since their time (Kölliker, Hensen, Loewenberg, Nuel, Gottstein, Lavdowsky, and Retzius), though some authorities have been unable to satisfy themselves that the spiral fibres are really nervous in nature (Rosenberg, Boettcher, Waldeyer, and Middendorp). With the latter group my own investigations compel me to place myself, for they have led me to the same conclusion arrived at by Waldeyer in 1870. I am fully convinced that there are no bundles of *spiral nerve fibres* in the cochlea such as Deiters, Hensen, Gottstein, Nuel, Lavdowsky, and others have described. *Cf.* Deiters (69), Taf. VII, Fig. 28, and Taf. VIII, Figs. 34 and 36; Nuel (206), Pl. IV; and Lavdowsky (178), Taf. XXXV, Figs. 5, 12, 13, 20. As to the existence of such structures as are here displayed there can be no question. I have often had the counterpart of Deiters' Fig. 28, Pl. VII, but the fibres there shown are not nerves, but connective tissue fibres belonging, as I believe, entirely, and, as I have demonstrated, at least in part, to the basilar membrane. Nuel's figures show mostly fibres of a different nature microscopically; but although I have seen such fibres as he offers in the figure on Pl. IV only a few times, they appear to me to be connective-tissue fibres modified by the reagents used and more or less transposed during the preparation. It should be recalled here that the radial nerve fibres after they leave the habenula perforata do not run in straight lines, but suffer two sorts of displacement, one of which is due to the spiral growth of the cochlear canal, by means of which the relations of all the contained structures are considerably distorted in a plane parallel to the basilar membrane, and the other of which is an easy undulation of the nerve fibre itself. This undulation of the

nerve fibre I have seen in all preparations showing the nerves, but since the nerves are invisible without previous chemical treatment, it by no means follows that the undulations exist during life; still it is not improbable that this is the case since such a disposition is not uncommon in the smaller nerves in the tissues of other organs. The various authors who have described the system of spiral nerve fibres do not agree among themselves as to what constitute the complete system or where the various bundles are to be found. No one has yet been able to trace the connection between these so-called spiral nerve fibres and the hair cells. Boettcher, whose extensive researches into both the embryonic and adult structure of the cochlea entitle his opinion to great consideration, calls attention to the logical inconsistency of the accounts of the authors describing these courses of fibres, in that they fail to find the origin and end of the spiral nerves and they do not agree as to their position and characters. No one has yet claimed that these tracts of spiral nerves have any representation in any of the other sense organs, nor has their existence been shown in the ear of the Alligator, in which type the mammalian organ exists in a much simpler condition than in any of the mammalia. From what I have already seen of the cellular structure of the Alligator's cochlea I am confident that spiral nerves occur neither in the sauropsid nor in the mammalian organ of this animal's ear. Waldeyer says in his resumé of the controversial points of the mammalian cochlea: "In stating my views in regard to the cells and fibres which are the subject of dispute, I will say that the observations which I have made with positiveness in regard to the nerve endings make it probable that neither the granule cells [*i.e.* the epithelial lining of the sulcus spiralis internus; these are the cells which Waldeyer had compared with the inner "granule layer" of the retina] nor the spiral fibres have a nervous character; otherwise we should be obliged to claim a double nerve ending. The difference between the well-established radial nerve fibres and the spiral fibre bands opposes this supposition. Still this point can only be determined by further careful examinations based on embryological researches."

Boettcher's monograph on the development of the mammalian cochlea appeared after this was written, though the researches were actually carried out some years before, and Boettcher's

conclusion was that both theoretical considerations and the embryological data were against the nervous nature of these spiral bands of threads.

In his earlier account of some points of cochlear anatomy, Nuel (207) described in great detail the system of spiral nerve fibres, and noted the following important fact which vitiates the theory of spiral nerves in the organ of Corti: "Eine Merkwürdigkeit von diesen Fasern muss ich noch erwähnen, nämlich auch in Bezug auf diese Fäden finden wir das System der Hörzellen in den äusseren Stützzellen vorgebildet, dem ich fand ein ganz identisches System von spiralen Fasern zwischen den Stützzellen, die, wie gesagt, den Hörzellen schon analog gelagert sind."

The fact that the so-called spiral nerve bands are well developed in connection with non-sensory cells casts doubt upon their nervous nature. I believe the "spiral nerves" exist in the living condition as delicate walled but relatively large lymph channels which are formed between the bases of the cells, and which are found not only in the organ of Corti and the Sauropsid organ, but also in the organs of the lateral line and the sense organs of the ears of fishes. In Petromyzon such a lymph channel is well developed in the surface canal sense organ (Pl. VIII, Fig. 11), and I have figured the lymph vessel under the inner row of outer hair cells of the pig on Pl. III, Fig. 10. There are numerous moniliform threads shown here, but they are part of the wall of the lymph space, and are not nerves, but connective-tissue fibres. These lymph spaces contract under the influence of reagents along with the other parts of the organ, and then appear in cross section, not as intercellular spaces, but as granular bodies placed on or near the bases of the hair cells; and this appearance is what Retzius has figured in sections of the mammalian cochlea. The fibres do not stain in Dogiel's methyl blue, and osmic acid does not differentiate them from other fibres of undoubted connective-tissue nature. The varicose fibres have appeared most distinct under low powers and after alkaline reagents. Finally, the evidence of comparative anatomy is entirely against the existence of these spiral nerve bands.

From the foregoing account of the cochlear ridge in the Hydrosauria and in the Mammalia it appears that a large number of cells outside of the last row of external hair cells seem

to be non-sensory in character. Hitherto, at any rate, they have been classed as supporting cells and non-sensory. They have never been shown to have hairs upon their cell caps, though these same cell tops separate from the cells much as the tops of the genuine hair cells do. They have never been shown to have nerve connection, though it is difficult to understand why they should be so well developed and in such abundance if they have no function beyond forming a ridge-like body; for it cannot be longer seriously held, I think, that all these strongly developed cells, forming more than half the bulk of the ridge of Corti, are merely supporting cells. Why should the organ need so much "support" on one side only? The cells are found only on one side in abundance, and on the side where they are fewest embryology shows us they are the degraded hair and supporting cells of an atrophied sense organ. In some parts of the Cortian auditory ridge these cells appear hypertrophied as compared with the hair cells themselves. If they are not all supporting cells, may not some have a sensory function, since they belong to a ridge supplied abundantly with nerves? I think it more than probable that renewed search will show that these cells are, part of them, connected with the fibres of the auditory nerve, and perhaps bearers of sensory apparatus on their upper ends. A careful analysis of the elements of Loewenberg's net and the membrana reticularis may reveal more than we yet know of the nature of these numerous well-developed cells.

The second topic is that of the peripheral endings of the radial nerve fibres. As Waldeyer has truly said, anatomists have described every known method of nerve ending as having been found in the cochlea. Since Deiters' time, however, there has been a general agreement that the radial nerves ended in hair cells as *one* of their endings. Of the other supposed endings we have heard less, the more thoroughly the Cortian organ has been studied, and to-day it may be considered practically settled that the radial nerves end only in the hair cells of the inner and outer rows.

The exact manner in which the nerves terminate in the hair cells is still an open question. Lavdowsky maintains that the nerve fibres more frequently end in the hair cells in the neighborhood of the nucleus than at their lower ends.

The nerve fibre penetrates the cell and ends in the protoplasm near the nucleus or in the nucleus itself, as he thought he had found. In young animals the nerve may present the appearance of ending bluntly against the side of the cell. This mode of ending is the one almost exclusively figured by Retzius for all the forms he studied, both adult and embryonic.

The latter author is specially positive that he has never observed anything approaching a penetration of the nerves into the cell protoplasm, and concludes that the nerve fibre merely applies itself to the surface of the cell wall by a more or less swollen and uneven plate. This contact is not easily destroyed, but Retzius thinks that there is no actual fusion of nerve substance with cell substance.

He says (237, II), p. 368: "Wie endigen nun diese Fasern? Hier bleibt eben die grösste Lücke in unserer Kenntniss vom feineren Bau des Gehörorgans. Ich habe mich vielfach bemüht, diese Lücke auszufüllen, bisher aber fast vergebens. So viel ist jedoch sicher, dass die unteren Enden der äusseren Haarzellen die oberen Fasern der Spiralzüge berühren und ihnen sogar anhaften; einen directen Uebergang der Nervenfasern in die Haarzellen sah ich aber nie; nie sah ich die von Nuel beschriebenen, nach oben zu den Haarzellenden hin emporsteigenden Nervenfasern. Diese Hauptfrage der Histologie des Gehörorgans der Säugethiere muss meiner Ansicht nach noch als unbeantwortet betrachtet werden." While I do not doubt that the last word has not been said on this topic, my own conviction is that in all the vertebrates I have studied, in this particular, spiral nerve courses do not exist, and that the fibres which pierce the floor of the canal make their way as directly as circunstances allow to the morphological bases of the hair-bearing cells and enter into such a union with them that a protoplasmic continuity is established between all living parts of the cell and the nerve end, and that there exists in the cell a specially arranged mechanism for the transfer by transformation of the mass motion of the endolymph into the molecular motion of the nerves.

Within all of the hair-bearing cells, and apparently running from cell cap to nucleus and from nucleus to basal end of the cell, are to be seen, especially well in cells killed in chromic solution, but also after the reaction of other chemicals, extremely

delicate moniliform threads, in number varying considerably so far as appearances go; the extremes of variation, though difficult of determination, are about the same as those of the hairs borne by these same cells. These filaments I propose to call the capillo-nuclear and the nucleo-neural filaments, and I hold that they are continuations of the nerve into the hair processes. Whether they pass through or around the nucleus is a matter which I have not succeeded in demonstrating. The first account of these structures which I find in the literature is that given by Boettcher (31), who describes these central fibres of the cell in the following words: "Ich habe früher Angegeben, dass in ihnen [*i.e.* the hair cells] ein glasheller centraler faden enthalten sei, welcher den Kern umfasst und selbst von einer blassen Hülle umschlossen werde, aber schon damals ausdrücklich hervorgehoben, dass sie im frischen Zustande anders erscheinen. Von spätern Beobachtern hat ausser Henle, Niemand auf diesen Centralfaden Rücksicht genommen. Letzterer bestätigt es dass, wie ich mitgetheilt hatte, die Corti'schen Zellen in verdünnter Salzsaüre die von mir beschriebene Form annehmen, meint jedoch, 'dass die Umwandlung Folge einer Gerinnung des Zelleninhalts sei.'

"Damit ist die Sache, glaube ich, nicht abgethan und jene eigenthümliche, immer in derselben Weise wiederkehrende Veränderung der Corti'schen Zellen nicht erklärt. Es liegt mir fern behaupten zu wollen, dass das Bild, welches Man nach der Salzsaurebehandlung erhält, dem normalen Zustande entspreche, auf andern Seite kann ich aber auch nicht zugeben, dass ein durchweg gleichmässiges Protoplasma constant in der Weise gerinne, dass es einen central verlaufenden glänzenden Faden bildet. Wir haben oben gesehen, welche Unterschiede die Bogenfasern im frischen Zustande und nach ihrer Behandlung mit Salzsäure oder Chromsaure darbieten. Auch hier existirt eine Hülle, die bisher übersehen worden ist.

"Aehnliche Verwandlungen eines besonders organisirten Theil der Zelle dürften bei dem Auftreten des Centralfadens der Corti'schen Zellen vorauszusetzen sein. Hiernach kann ich die Annahme nicht Raumgeben, dass derselbe ein Gerinnungsproduct sei, glaube vielmehr, dass er auch im frischen Zustande vorhanden ist und vielleicht in Form feinster Fasern durch die Zelle verläuft, in Folge der Behandlung mit Salzsäure

aber erst als dickerer glänzender Faden hervortritt." These observations show that Boettcher did not see the fibres as I have found them, although on general grounds he thought the single coarse fibre might be composed of finer ones drawn together by the contracting action of the reagent, or swollen till they coalesced into one large rod, as is more likely to be the case when hydrochloric acid is used. My discovery of these numerous moniliform threads was made entirely independently of Boettcher's investigations, as I had not been able at that time to consult his paper so rich in accurate observations.

Boettcher's observations have not received their just recognition at the hands of anatomists. Their full value for the physiologist we may not now properly appreciate, but that we shall in the near future in greater measure than in the past I do not doubt. My own observations enable me to go much further in theory than Boettcher dared to go, as they carry the morphological basis much further and render the relations of nerve and nerve-end cell much more intelligible than ever before, and enable us to demonstrate a physically continuous protoplasmic path from the percipient element in the ear to the receiving centres in the brain. That this is a gain for the experimental physiologist, as well as the speculative physiologist, is apparent enough.

Other investigators have searched for these filaments, but have not found them. Nuel (206, 1878) was not successful in demonstrating their presence, and considered them artifacts.

Paul Meyer (192, 1876) says: "Jamais nous n'avons pu constater de liaison aucune entre cette cupule et le noyau de la cellule.

"Du reste, ainsi que le montrent les imbibitions par l'acide osmique ou par des matières colorantes, nous avons affaire ici à un véritable corps solide, et c'est ne pas une simple illusion d'optique, comme semble l'admettre Retzius, d'après lequel ce disque terminal ne serait du qu'à un jeu de lumière sur la partie supérieure plane ou un peu excavée de la cellule.

"Cette cupule solide porte les cils terminaux; les deux ne constituent qu'une même masse." Meyer did not observe this terminal body to be connected with the nucleus of the cell; on the other hand, as he expressly says, "nous n'avons eu sous les yeux une préparation nous permettant d'affirmer nette-

ment une continuation directe entre le noyau de la cellule et le filet qui y pénètre par l'extremite inferieure," *i.e.* the nerve fibril which, according to Meyer, comes into close contact with the cell, — fusion with cell wall, — but does not penetrate into its protoplasm.

In describing the hair-bearing cell from the comparative standpoint, Hasse says (*loc. cit.* p. 77): "Am freien Ende trägt jede Zelle einen homogenen, cuticularen Verdickungssaum, ähnlich wie die Darmcylinder und aus demselben erhebt sich ein ebenfalls als cuticulares Gebilde anzusehendes, namentlich bei den Fischen ungemein langes, steifes, Kegelförmiges, unendlich fein auslaufendes Haar, dessen Basis, wie erwähnt, Längsstreifungen zeigt, die warscheinlich der Ausdruck von Stiftchen sind, die von der Basis der Haare gedeckt werden und vielleicht mit den Nervenenden in Zusammenhang stehen, da ich glaube, dass die an das basale Ende der Gehörzelle herangetretene Nervenfaser vielleicht unter Theilung das Centrum der Zelle bis zum cuticularen, Verdickungssaume durchsetzt und nun entweder in die Basis des Haares tritt, oder vielleicht auch in einem Korperchen endet, auf das Hensen im peripherischen Theile der Zelle unter dem Verdickungssaume zuerst aufmerksam gemacht hat. Die ins Epithel getretenen Nervenfasern gehen entweder als blasse, ungetheilte Axencylinder an das untere Ende der Hörzellen, oder theilen sich, innerhalb des Epithels einen intraepithelialen Plexus bildend und oft auf weite Strecken horizontal verlaufend, in mehrere Aeste, bei den höheren Thieren in zwei bis drei, um dann zum basalen Ende der Gehörzellen zu treten."

And further on, page 93, in describing the conditions found in mammals, he says: " . . . aber jedenfals hier nicht enden, sondern wahrscheinlich durch das Innere der Zelle bis zu dem basalsaume und vielleicht durch diesen bis zur Basis des Gehörhaares und den Stiftchen verlaufen."

A study of these filaments in the hair cells of the organ of Corti in the ox, cat, dog, pig, and rabbit enables me to give the following details of their arrangement and relations. The capillo-nuclear fibres, to begin at the cell cap, appear to be continuations of the bases of the hairs, and in this region, together with the cell caps, have given rise to the structure discovered and described by Hensen (1871, 129), and which by later authors

has been called Hensen's body or nucleus. Hensen found in the top of the outer hair cells an ovoid refractive body somewhat smaller than the nucleus of the cell, variable in size, which seemed to be surrounded by spirally arranged threads, which, notwithstanding its minute size, recalled nerve end bodies and bulbs to our author's mind. Although he usually found it near the upper end of the cell in close relation to the cell caps, he also found it at all distances between the upper end and the nucleus (Pl. V, Figs. 4, 5, 7, and 8; Pl. X, Fig. 4; and Pl. XII).

This body presented the appearance of a thin walled ovoidal capsule encircled by a fine, evenly, spirally wound fibre. Below this ovoid body, and usually in contact with it, he found still another small round nuclear body, which he thought was, under normal conditions, inside the cell. It is impossible to say what the cause of the peculiar form of the cell's central protoplasmic mass in Hensen's preparations may have been, but I think there is no reasonable doubt that Hensen had under his lens merely a modification of the structure discovered by Boettcher and later observed by Henle, and which I have myself undertaken to describe more fully. The normal condition of this part of the cell, so far as the capillo-nuclear filaments are concerned, is then as follows: The upper end of the cell is filled with a clear protoplasm, more fluid at the circumference and between the threads which lead downwards from the bases of the hairs to the nucleus. These filaments appear to be connected with the nucleus. Whether or not they are so connected is not to be determined readily in the whole cell, but in sections, or, better still, in teased preparations where the parts of the cell are more or less separated from each other. The surface of free nuclei may be seen to be studded with projections, due apparently to the remnants of protoplasmic filaments penetrating the nucleus from the cell protoplasm. In Fig. 8, Pl. V, is shown such a free nucleus, in which the projections are separated into two sets, each set occupying the polar part of the upper and lower hemispheres of the nucleus respectively. On either side of the nuclear body are two smaller, deeply stained, spherical bodies without visible connection with the nucleus. These two bodies lie opposite each other in the equatorial zone of the nucleus which is free from the projections spoken of above. The struc-

ture and functions of the small paranuclear bodies is entirely unknown.

The filaments either pass into the nucleus or are closely applied to its surface as they pass it by. Considering the fact that the nucleus itself presents an appearance in harmony with the actual penetration of the capillo-nuclear filaments, it is not out of the way to conclude that there is such structural relation between these sensory fibres and the body of the nucleus. The fibres which leave the nucleus over its lower hemisphere arrive in due course at the bottom of the cell, and are only separated from the nerve end by the cell membrane. It is admissible, however, that these nucleo-neural filaments may with truth be called the prolongations of the nerve inwards to the cell nucleus; but that is a minor consideration as compared with the fact of the actual connection of the two ends of the cell by direct protoplasmic paths of such definite arrangement as to leave no doubt of their general nature as mediators between the percipient cochlear hairs and the transmitting cochlear nerves.

Since the above was written I have received a paper by Dr. K. C. Schneider, entitled "Untersuchungen über die Zelle," in *Claus' Arbeiten*, IX, 2, 1891, in which the author shows that such a condition of the nucleus as I figure in Pl. V is the ordinary condition for all cells. The author further describes the relations of the nuclear and cellular protoplasmic motile filaments at length, and figures on Pl. I, Fig. 7, the projection of vibratile cilia beyond the surface of the cell, *i.e.* through the cell wall, and their continuation centred into the nucleus. As such a condition is the normal one for the *Infusoria*, it is not at all strange that in the sensory structures of higher animals the extra-cellular projections should be continued structurally into the nuclear network. Schneider's definition — or perhaps I should say *demonstration* — of the nature of the cell wall enables us to readily conceive how the nerve threads (I do not mean axis cylinders, but the ultimate threads resulting from the breaking up of such a nerve end as we encountered in the case of the hair cells) may easily penetrate into the cell, *or even establish protoplasmic continuity without so penetrating*.

So that we are not compelled to make the assumption of a penetration in order to establish an actual continuity of the two

structures, such as shall be effective in mediating between the nerve-end organ and the nerve.

In concluding this paragraph I wish to propound the definite thesis that there is an unbroken protoplasmic path from the base of the hair cells to the brain cells, along which path the auditory stimuli travel, and during which time and before leaving the end cell they are transformed from mass motion to molecular motion.

After having traced the cochlear organ from the Fishes up to the Saurians, and described its sudden and very remarkable development in this group as exemplified in the Alligator, and after having studied in some detail the main characters of the higher mammalian ear, the determination of the characters of the monotreme cochlea has become a truly enticing topic for investigation.

Urban Pritchard (216, 1881) has done the only work, of which the results have been published, on the anatomy of the membranous cochlea of the Monotremes, but his observations, although valuable, are not so complete as we need at the present time. The membranous cochlea is of course shorter (apparent length) and smaller than the bony tube, but a very good idea of its length may be had from the size of the latter.

Pritchard gives one-fourth inch as the length of the bony cochlea in *Ornithorhynchus paradoxus* (more accurately 6.3 mm.). However, on account of its curvature around the end of the lamina spiralis ossea, its entire length is greater than that of the bony cochlea. It runs nearly horizontally forwards and curves at the same time slightly outwards. The lagena appears as a swelling on the cochlear tube, much as in Saurians (Alligator, Crocodile) and Birds. It has a greater diameter than the rest of the cochlear tube, and is flattened parallel with the plane of the basilar membrane. The Sauropsid characters of the Ornithorhynchus cochlea are then more prominent than the mammalian so far as the general shape is concerned, but when we come to the internal characters we find them so far as known strictly mammalian.

The Sauropsid organ has disappeared; the mammalian organ of Corti is well developed, but possesses two rows of inner hair cells instead of the *one* usual among other types of mammals. The neural cartilage of the Sauropsid ear has been converted

into the lamina spiralis ossea and supporting bone. The cochlear canal is triangular in section throughout most of its course, and has the same general position within the lymphatic space formed by the two scalæ — s. tympani and vestibuli — that it has in the higher mammals. The basilar membrane is a three-layered, relatively thick plate. The lower layer is composed of longitudinal fibres with spindle-shaped nuclei; the middle layer contains transverse fibres, while the upper layer is composed of fine transverse fibres.

The pillars of Corti are well developed, and they inclose a triangular tunnel much as in mammals generally. The pillar feet of the inner and outer pillars are very similar in shape and size, but the enlarged heads differ; that of the inner rod is oblong in shape with a delicate process projecting inwards from its upper part, while that of the outer pillar is rounded and fits into a hollow of the head of the inner rod. As Pritchard found the hair cells, each one appeared to bear on its upper end four or five stiff and relatively thick bristles — the auditory hairs.

The hair cells are well-defined structures with flat, circular tops, from which the stiff hairs rise, with large nuclei imbedded in a granular protoplasm.

The supporting cells are well developed, and extend from the basement membrane quite to the surface of the sensory ridge.

After having left their channels in the lamina spiralis ossea near its lower border, the nerves pierce the upper layers of the lamina spiralis membranacea (basilar membrane), forming in so doing the usual habenula perforata. The nerve fibrillæ pass upwards and outwards to the inner hair cells, and the latter or outermost fibres, after crossing the canal of Corti, end in the outer hair cells. The mammalian organ does not extend further towards the apex of the cochlear tube than the lamina spiralis ossea, and here the tube narrows, to suddenly enlarge again into the lagenar pocket, which is curved around the open space called the helicotrema, by means of which the two perilymphatic spaces communicate. The lagenar sense organ in Ornithorhynchus is found to be in structure much like the maculæ of the utriculus and sacculus of this animal's ear, but more like the lagenar organ of the Sauropsida. The usual otolith collection is present on the surface of the sensory hair field.

The cochlear ganglion is inclosed in the bony plate, along the inner border of the cochlear floor as in other mammals.

The rods of Corti are placed on the basilar membrane at a much sharper angle than they are in the higher Mammalia, in consequence of which the canal of Corti is less broad than usual in this class. This condition I consider to be more primitive than the adult condition of the higher Mammalia, as the latter forms pass through a stage identical with this, which occurs in late embryonic life.

Pritchard's deduction with reference to the homologies of parts between the cochlear channels of Ornithorhynchus and the higher mammals contains a grave error due, in the first place, to his misconception of the true nature of the cochlear tube especially, as well as of the so-called scalæ, and secondly to ignorance of the actual conditions existing in Birds. He says (*loc. cit.* p. 278): that the lamina ossea of Ornithorhynchus (and other mammals) corresponds to the avian quadrilateral cartilage, and that the mammalian ligamentum cochleæ is represented in the Bird by the triangular cartilage. Also that, whereas the lower division or scala tympani of each corresponds, the ductus cochleæ of the Bird occupies the whole of the upper division, and therefore corresponds to the scala vestibuli and scala media (or ductus cochleæ) of the mammal."

That the cochlear tube of the avian ear possesses well-developed scalæ tympani *and vestibuli* is such a well-published fact that one is at a loss to understand how Professor Pritchard could have overlooked it; besides which, any transverse section of the bird cochlea prepared with ordinary care would have prevented the above blunder.

The general rule which Hasse laid down that "wenn einmal ein Theil mit einer macula oder crista acustica mit Nervenendapparaten des Hörnerven differenzirt ist, dieser nicht verschwindet, sondern, namentlich wenn er die Schnecke angehört, in der Wirbelthiere reihe immer mehr entwickelt," is no longer to be considered as stating the usual course of events; for of three important exceptions to his rule the most important one affects the strongest clause in the rule, viz. that concerning cochlear organs. Unaccountable as it still is, the fact remains that the largest and at one time most important cochlear organ does disappear from the mammalian cochlea about the time of birth,

after the forces of the organism have been expended in building it up to a state of physiological perfection, while its place is taken by an organ very similar to it in the earlier stages of its development, but which, it must be admitted, develops along a different line from the Sauropsid organ. Of the greatest importance in tracing the descent of the mammalian ear from the Sauropsid condition is the recognition of the fact that at least two species of lower mammals retain the papilla acustica lagenæ in a condition of development entirely identical with that found in Birds and Hydrosaurians. The existence of the crista acustica abortiva has not been determined in the Monotremes.

An *explanation* of the origin and significance of the pillars of Corti at once in harmony with their origin and with their function, as I conceive it, and as it seems clearly indicated by the new light we have received as to the nature of the whole organ, is that, *owing to the increasing length of the hairs of the hair cells, there arose need of greater isolation and firmer support.*

The inner hair cells, being the oldest row, are first affected and first supplied.

There are indications of a progression of this process outwards, between the rows of the so-called outer hair cells, and there is evidence (see Pl. X, Fig. 4) that this process has already begun in the organ of Corti of the Alligator: it is here seen between the innermost and the second rows of hair cells.

The pillars of Corti are then isolating and specially and peculiarly constituted supporting structures. As the ear differentiates we may expect similar pillars to form between the second and third, and third and fourth rows, as well as between the latter and the fifth or outermost row of hair cells.

There is evidence that the number of rows of hair cells in the mammalian cochlea is on the increase. All the facts point to the conclusion that the number of rows is increasing at the same time that they are becoming more highly modified, *i.e.* specialized and capable of executing the functions of the organ in ever-increasing degree of perfection.

The Alligator's organ of Corti shows a larger number of rows of hair cells than the mammalian organ, and all mammal forms which have been studied so far show unmistakable indications of the increasing differentiation of the organ of Corti. In the

Alligator we find that the nerve distribution is, as far as the external branch is concerned, fundamentally the same as in mammals. For instance, in the Alligator the nerve enters through the cartilaginous supporting bar at the inside of the Sauropsid acoustic papilla, and piercing the cartilage passes out underneath the inner hair cell row, to which it gives off fibres, under the main plate of the cochlear organ, and here disappears at the bases of the cells. As the fibres approach the bases of the hair cells, which here rest on the cushion formed by the supporting cells of the organ, they lose their medullated sheaths, and passing upwards, pierce the upper layers of the supporting cushion, reaching finally the bases of the hair cells, probably penetrating into their substance, and entering into direct communication with their nuclei as in the mammalian cochlea. The fibres which pass beyond the row of inner hair cells cross obliquely the space outside these cells and disappear among the outer hair cells. The hairs which are given off at the top of the cells appear to be thicker and shorter than the hairs of the corresponding cells in the mammalian ear, and consequently the membrana tectoria which they form is a wider band relatively, but neither absolutely nor relatively as thick. It is also thickest in its middle part, thinning off both ways.

The inner row of outer hair cells of the mammalian cochlea shows much more than the inner hair cells, the same form of body and relation to supporting cells and basilar membrane that the remaining hair cells of the organ of Corti display; indeed, they may be said to have progressed beyond them but little except in the more perfect isolation of the cells and the consequent greater separation of the hairs of the row. The isolation cells are not so distinct and do not play as important a part in the separation and support of the cells beyond the second row as they do between the first two rows of inner hair cells; they are, however, much advanced beyond the condition of development, in which they exist between the cells of the outer, unmodified portion of the papilla basilaris. Here they present the simple unmodified condition which characterizes them in the maculæ, cristæ, and papillæ of the other parts of the ear.

The pillars of Corti present in their development among the

Mammalia an epitome of their phylogenetic history, and in the embryo mammal we may recognize the reptilian condition as illustrated in the organ of Corti of the Alligator ear. These cells appear to be well formed and separate the first two rows of hair cells, but they do not possess such marked fibrous structures as are present in the mammalian pillar cells. The blood-vessel which runs below the floor of the organ (formed by the basilar membrane) is present practically as in the mammalian ear.

Connected with the pillars of Corti and forming a part of its supporting framework is a structure formed by the cell caps of the supporting cells on either side of the pillar row, and which, from its appearance when isolated, has been called very appropriately the membrana reticularis.

I am confident that the reticular structure is a product merely of the cell caps of the supporting cells,[1] and that the intercellular substance, if such exist, is not important in the formation of its framework. The hair cells are only lightly attached to the supporting cells. Everywhere except in the region of the reticulate membrane they are separated, in fact, by considerable interspace, but in this region the cell caps of the hair cells seem to fill interspaces or the reticula of the membrane; and since the tops of all the cells of the organ lie close together and form a mosaic, and since the supporting cells adhere very tenaciously to one another by their cell caps, it is very easily understood how the structure may appear as a discrete structure, after the organ of Corti has been passed through the processes of preservation, hardening, staining, clearing, dissecting, and mounting, one or all, before observation.

The membrane has no individual existence any more than the membrana tectoria, and with this we have removed another feature of the cochlear anatomy, which appeared to show a want of harmony between the type anatomy of the canal organ and that of the highly modified Corti's organ.

[1] The reticulate membrane very frequently retains the cell caps of the hair cells within its meshes, but under the definition they are not to be considered constituents of this structure. From the new standpoint they are on the same footing with the isolation cells as contributors to the reticulate frame. That the hair cells are less firmly fixed by their upper ends is apparent from the greater ease with which they separate from the membrane.

The essential elements of the organ of Corti are, then, —

The *hair* cells — Percipient elements.
The nerve cells and fibres — Transmitting elements.
The supporting cells — Isolating and supporting elements.

These three include the only structures that are necessary for the performance of the physiological function of the cochlea, notwithstanding previous physiological speculations with respect to the necessity of a damping apparatus and of a vibrating membrane composed of separable but fixed cords, *because they are the only structures present which can possibly have to do with the auditory function, and they also represent the structures present in the type organ, from which they have descended.*

Concerning the nervous elements in the mammalian organ of Corti, there is still much uncertainty as to the exact distribution, the number, and terminations of the fibres of the cochlear nerve entering the organ through the limbus spiralis. There is substantial agreement, however, as to the main facts of nerve supply so far as course and general disposition of the nerve fibres of what may be called the direct system.

We know enough about the matter to entitle us to enter into comparisons with the lower forms, more especially those which have been investigated up to date, and whose organ of Corti presents as many rows of hair cells as are found in man. In those cases in which the rows are not numerically as strongly marked as in man, the cochlear organ appears to have lagged behind in its development. It is true some forms have a greater number of spiral turns to the cochlea without at the same time actually having larger cochlear organs, *i.e.* increased number of percipient elements. For, manifestly, it is not sufficient in estimating the number of hair cells in a row to simply count the number of complete turns of the cochlear tube and reckon on the basis of the number of cells counted in the spiral turn of some one form chosen as type. For the length of the curves, *i.e.* the openness or closeness of the spiral, involves the circumference of the complete ring of the spiral, and hence the number of cells contained in it.

It is evident that greater isolation of the hair cells of a compound sense organ, and thus of their percipient hairs, is obtained by the elongation of a few rows of cells, with the scant

development of the remainder, than by massing together the whole large number of cells into a compact plate as in a macula or a papilla, as occurs in most of the sense organs of the ear. I conceive the cause which lies behind the remarkable growth of the cochlea in length and spiral course to be the physical necessity for the isolation of the cells and the greater perfection, the increased delicacy and sensitiveness for perception of the hairs borne by the cells.

THE HAIR BAND (MEMBRANA CORTI, MEMBRANA TECTORIA).

1. Historical.
2. Form and Relations of the Band to the Cochlea.
3. Sensory Hairs.
   - *a.* Disposition in the band. Relation to the sensory cell.
   - *b.* origin.
   - *c.* number.
   - *d.* course.
   - *e.* normal relation to scala media.
   - *f.* size at base and tip and relative lengths of hairs in different parts of the organ of Corti.
   - *g.* intercapillary substance.
   - *h.* comparative.
4. Loewenberg's Net.
   - *a.* position and extent.
   - *b.* size of net and meshes.
   - *c.* origin and attachments.
   - *d.* varieties and variations in same cochlea.
   - *e.* composition of the cords of the meshes.

All students of the anatomy of the vertebrate ear down to the time of Ecker and Reich had failed to find in the chambers of the ear cellular structures of a specific kind, and almost all of them considered the ear to be more or less completely filled with a gelatinous matter which was specially well marked in the ampullæ and over the maculæ, — in connection with the jelly otoliths were frequently found. F. E. Schultze in 1858 first described the ampullary gelatine as a crest of long, straight, auditory hairs, as he called them. It is true Ecker, and later his student Reich, had found the ciliate epithelium of the Petromyzon ear, but they did not discover the true auditory

percipient structures. Although Schultze's observations were accepted by competent authorities as correct, the older idea of the presence of the auditory jelly was only slightly affected; and while there was nothing in Schultze's observations to give color to the view, it was held, however, that the auditory hairs, although undoubtedly present, did not project into a lymph-like liquid, but were received into canals or other openings within the gelatinous mass later called a "cupula terminalis." The cupula terminalis was thought to be a secretion of the non-hair-bearing cells of the sensory area. This idea gradually grew, and was extended to the covering structures of all the auditory sense organs, which were variously termed the membranæ tectoriæ, otolithic membranes, or reticulate membranes. The special term applied by Lang to the gelatinous mass of the ampulla was the *cupula terminalis*, and it was not until 1878 that the whole error was overthrown and the complete meaning as well as the entire accuracy of Schultze's observations was demonstrated for the ampullar sense organs. Hensen, to whom we owe this important demonstration, worked single handed against the most determined resistance on the part of his contemporaries, and it was only after several years' time, during which he repeated his own observations and republished his account with additional facts and evidence, that he forced those of different mind to admit that their ideas of the relation of the sensory hairs to the ampullar cavity were entirely erroneous and that the microscopic preparations of the ear sense organs, which they supposed fully proved their position, normal though they seemed, were *artifacts*, creations of their own unconscious efforts, which although made, it must be admitted, in most if not all cases, with the express purpose of getting at the truth, were none the less destructive of the truth and constructive of false conditions and conceptions.

The demonstration by Lang of a dome-shaped, striated (sometimes apparently homogeneous) mass resembling stratified jelly, led him to publish his cupula terminalis idea, and the ease of demonstration and apparent constancy of the structure after ordinary histological preparation led off other workers only too completely, until Hensen took up the subject and studied the ampulla under conditions as natural as it was possible to obtain, with the result already mentioned.

Max Schultze (1858, 256) discovered the auditory hairs of the cristæ acusticæ of the fish ear (Teleost). He found them projecting freely into the endolymph.

Franz Eilhard Schulze (1862, 255) re-examined the question, and found that Schultze's observations were correct so far as they went; but he discovered that the hairs were much longer than Schultze had described them to be. They were equal in length to at least one-half the diameter of the ampullæ, and probably were even considerably longer.

Lang (1863, 175) found in preparations of the ampullæ treated with hydrochloric acid and alcohol that a finely striated mass, which he called the "cupula terminalis," covered the auditory crest. He considered the auditory hairs, previously described by Schulze and others, to be artifacts resulting from the transforming action of the acid and alcohol on the cupula.

Hensen (1863, 130) confirmed the discoveries of Schulze, and Hasse (1870, 116) accepted the arguments of Lang, but regarded the hairs as relatively short structures.

Retzius (1872, 238) agreed with Lang and Hasse.

Paul Meyer (1876, 192) was in essential agreement with Hasse and Retzius.

Dr. Kuhn (1877, 170) found in the ampullæ of all the species he worked upon (fishes, amphibia, and reptiles) what he considered to be a cuticular structure of such form and extent as to serve as a dome-shaped cover of the crista and its sensory hairs, effectually shutting off the hair chamber from the rest of the ampulla. This organ — the so-called cupula terminalis — was of form and structure varying with the species studied.

Kuhn says (*loc. cit.* p. 316): "An frischen Präparaten ist es unmöglich dieselbe in situ zu Beobachten; sie fällt von der crista ab und wird ihrer Durchsichtigkeit halber stets übersehen." In ears hardened in chromic or osmic acid, Kuhn was able to study the structure and relations of the body to the hair cells and to the crest. Even in these cases, however, the cupulæ were frequently absent wholly or in part. The base of the cupula was always found to be concave, repeating, as a rule, the curve of the crista acustica. He never found the *cupula projecting beyond the edges of the hair-cell territory;* and consequently any relation to the planum semilunatum was not to be thought of. The body of the cupula, rising from its concave

base, was dome-shaped, though, as Dr. Kuhn's figures show his preparations, this was by no means the constant form. Some of his figures, as Fig. 38, Pl. XX, show a form of "cupula" which was doubtless produced by the separation of the hair tuft near the apex of the crista, from which line of separation they fell flat to the floor of the chamber either way, forming in this manner a bilobed cupula that certainly does not appear "terminal." In the fresh cupula, Kuhn never saw the fibrous structure which appears in most hardened preparations, though not in all. He considered the fresh cupula to be composed of a homogeneous, more or less glassy, transparent, and refractive, gelatinous matter of slight resistance, in which no trace of striation was present. In most other matters of detail, Kuhn agreed with the previous investigators who had gone over the matter, Lang, Clason, Retzius, Meyer, and others; but he did not accept the conclusions of Hensen and Cissow. Kuhn separated the fibres of the cupula by teasing, and, as his figures show, obtained bodies of the shape and size of the terminal portions of the ampullar hairs.

Hensen (1878, 131) renewed his studies of the auditory hairs, and arrived at the following results: —

(*a*) In embryo Teleosts (*Gobius Ruthensparri*, *minor* and *microps*) from 40–45 mm. length, the hairs of the crista acustica project nearly if not quite across the ampulla (in length consequently equal to the diameter of the ampulla), and hence bear entirely different relations to the ampullar structures from those described by the authors who have touched upon this subject.

(*b*) In the living condition and in fresh preparations there is no ampullar cupula terminalis to be found.

(*c*) It is impossible that any solid matter is present within the ampullar above or among the hairs, for these may be seen to become applied so closely together as to leave no free space between them.

(*d*) On the contrary, the solid cupula terminalis is produced by the action of the reagent used, *e.g.* hydrochloric acid and alcohol (Lang), which causes the hairs to disappear as such, and converts them into gelatinous substance or a thick mucous liquid.

Retzius (1881, 237) described many capulæ terminales in the first volume of his extensive monograph on the ear of vertebrates, and held to his original views, extending his observations

over many species of fishes and amphibia. He considered the cupula to be a normal structural element of the vertebrate ampulla, since he had always found it as a sharply defined and regularly formed structure, on account of which he was unable to accept Hensen's views, though he distinctly states that owing to the fact that his observations had for the most part been made before Hensen's article was published, he did not give the latter that consideration which he now concedes was its just due. He had never found the auditory hairs free and long except in the case of Proteus, and this, to him, unusual condition he was entirely unable to explain in the light of the cupula terminalis.

Hensen (1881, 132) appeared again in print, denying in the most emphatic manner the natural existence of the cupula terminalis. He repeated his former observations and measurements of the auditory hairs made on species of Gobius, this time a younger fish, 10–30 mm. long, and arrived at the same results as formerly. Concerning the relations of the otolith hairs to the otoliths, he states that the latter are borne by the hairs 0.01 mm. from the surface of the epithelium. The small otoliths seem to be inclosed in a membrane, while the larger ones lack the membranous envelope. The coverings of the maculæ utriculi and sacculi, Hensen could not find; and so he declared those described by various authors to be artifacts.

The long auditory hairs of the ampullæ of adult Teleosts may be readily observed if the ampulla is carefully removed from the head, and examined under slight pressure. They may also be seen more or less well preserved in suitable sections. In the closed ampulla of *Pleuronectes sp.*, Hensen measured hairs 0.19–0.2 mm. The breadth of the ampulla over the crista was 0.5 mm. The actual length of the hairs was 0.4 mm. The hairs after removal from the ampulla measured (maximum) 0.12 mm.

Owing to thickness of the ampullar walls and pigment deposit the Frog's auditory hairs are invisible in the unopened ampulla. They measure 0.12 mm. when taken out, and are probably at least 0.2 mm. long in the uninjured state. Every motion of the water throws these hairs into the greatest confusion, tangling them in hopeless fashion; and they remain as a compact, gelatinous, spongy tissue or more solid mass. In this

condition they easily break away *en masse*, or stick to the walls. Hensen concluded that the hairs of the Frog end more pointedly than those of fishes, but that they also have heavier bases, with more sharply defined structural detail. Hensen confirms Retzius's discovery that the so-called hair from a cell is composed of many finer fibrillæ. In optical cross-section one is able to determine that the number of fibres which enter into the body of a round hair is about eighteen to twenty. The thickness of a single fibre is 0.0007 mm. Hensen found that in some species of Teleosts, if the ampulla was disturbed before killing and fixing with osmic, no cupula was formed. It was invariably present when the ampulla was hardened in osmic *in situ*. In other species the ampullæ would bear removal, and still give good cupulæ.

When such osmic cupulæ were hardened in Müller's solution, for twelve hours after fixing, it was found that they remained firmly fixed to the crista, contrary to the observations of other authors, with respect to lack of attachment of the cupula to the crista.

Hensen was enabled to observe the various stages of the formation of the cupula by the action of reagents, and to prove conclusively that it was gradually formed from the hairs or from the intercapillary substance. He was inclined to think that the latter matter was the source of the artifact and that the hairs projected up into it or were more or less bent outward before entering the gelatinous mass. The cupula of osmic acid is much different from the chromic acid structure (Kuhn's), or from the hydrochloric acid cupula (Lang's).

Retzius (1884, 237, II) gives up his former position, after a careful study of the problem, admits the truth of Hensen's position, but calls attention to the fact that the latter author assumes the presence of an intercapillary substance whose coagulation by reagents gives rise to the cupula, so that, as he thinks, Hensen really assumes the presence of a sort of fluid cupula after all. Although loath to give up his former views entirely, resting as they did on many carefully prepared ears and on their careful study both by himself and his friends, Retzius does so since he had observed the degrees of cupula formation.

My own observations lead me to deny the presence of a special intercapillary substance anywhere in the ear.

The brothers Sarasin (1887, 248, II, 2, p. 46) describe a mucous secretion which they found quite regularly in preparations of the sense organs of the Ichthyophis, which surrounded and extended beyond the sensory hairs, was unstained by borax carmine, and was undoubtedly excreted by the supporting cells, since the sensory cells all ended in sensory hairs, which precluded the formation of an excretion. They were unable to decide which of the supporting cells were concerned in the production of the secretion, and expressed the opinion that they all possessed limited secretory powers. The secretion thus produced may form a tubular process projecting beyond the sense organ and serving in a measure to protect it. This is the equivalent of the so-called hyaline tube so often described for fishes and larval amphibia by F. E. Schulze and others.

It hardly admits of doubt that the auditory club described by Sarasin brothers for the well-developed lateral sense organs which they consider accessory auditory organs is either a product of the sensory hairs alone, in which case it would be the analogue of the cupulæ, or of these and some additional substance. In any case it has nothing in common with the auditory otoliths.

As I shall show further on, the so-called supporting cells are in part true mucous cells, and the hyaline tube is a product of their genuine mucous secretion, its tubular form depending on the absence of the secreting cells from the centre of the sense organ. This secretion bears the same relation to the sense organ that the mucous canals of Elasmobranchs do to the ampullæ of Lorenzini, which lie at the bottom of canals, *i.e.* at their proximal blind ends.

The auditory club which these authors describe for the accessory auditory organs of the trunk region of Ichthyophis is very refractive, but is not a genuine otolith, since it lacks calcareous matter, and it is further not a true cuticular structure, since it swells in strong caustic potash and dissolves. They considered it to be a hardened glandular secretion, the product of the gland cells (*i.e.* supporting cells) of the organ, and functional as an otolith. The structure readily falls out of its cavity in manipulation so that sections are found without this structure.

The test of their view that these lateral line organs were accessory ears the authors found in the study of the ear itself, and

figure a section through the sense organ of the sacculus, and carry out a detailed comparison of the structures of the two organs. The auditory club is physiologically equivalent to the otoliths. Morphologically, however, the brothers Sarasin think it is more like the cupula terminalis which Lang, Kuhn, Hasse, and Kölliker, found in the ampullæ of the ear.

After thus briefly reviewing the history of the cupula terminalis, we are better prepared to estimate the value of the views which have been, and which in part are still held concerning the tectorial membrane of Corti's organ or the auditory damper of the physiologists.

Its discoverer, Marquis Corti (1851, 59), gave the following account of it: "Quant on observe une bandelette dentelée dans l'état le plus frais et le plus intact possible, on voit que la membrane très mince qui lui sert de toit et très tendue sur la bandelette même et ne présente jamais aucun plis. Cette membrane part, comme nous avons vu, environ du bord externe convexe de la bandelette sillonnée en couvrant les dents de la première rangée, et arrive à couvrir a peu près trois rangées de cellules épithéliales placées sur la zone pectinée," and he calculated the distance between the "bandelette dentelée" and the membrane to be about 0.0085‴.

Claudius (1855, 53) described Corti's membrane as a tolerably tough, but extremely thin membrane, finely striated with parallel markings; to him it appeared elastic. It begins on the inner border of the crista sulcata below the epithelium without apparent boundaries, covers over the crista to the teeth, and from the apices of the latter it stretches across to the periost of the outer cochlear wall, running parallel with the membrana basilaris. It inserts in the periost under the epithelial coat. It retains these characters in all parts of the cochlea.

Boettcher (1856, 29) wrote: "Corti's membrane stretches parallel with the membrana basilaris from the acoustic teeth to the inner surface of the outer cochlear wall, so that, together with the basilar membrane, it forms a closed canal."

Kölliker (1859, 167): Corti's membrane is composed of (1) a special striated lamella, (2) an epithelium, and (3) a delicate connective tissue. The striated lamella appears to be of connective tissue nature, is separable into a thinner and thicker portion. The thinner is transversely fibrous, the thicker striated (*i.e.*

fibrous) parallel with the long axis of the cochlea. The rounded end appears frequently canal-like, in which Kölliker thought he detected a blood-vessel in a few preparations.

Boettcher (1859, 35) defends his former views relative to Corti's membrane. He recognizes two zones, an inner and an outer. The inner is extremely pale, with pronounced cell markings (impressions). External to the acoustic teeth the second and thicker zone begins. It is very thickly and finely striated. On the external border of the latter zone one frequently finds broad branching fibres, which usually form the border, then bending at right angles are dissipated in a brush of branches, which pass inward and are lost in the fine striation. Not far from the border one frequently sees a seam which may perhaps mark the line of insertion of the third zone. Boettcher also had preparations which showed even a second membrane running across the scala media into the cochlear wall.

Deiters (1860, 69) described this structure as follows: "Corti's membrane does not begin at the apices of the cells, but passes on beyond them; but beyond the apices it is fine, transparent, and scarcely striated. External to the teeth it shows a diagonal striation due to folds or fibres. The outer border of the membrane really inserts on the ligamentum spirale. The upper surface is covered by a simple, thin, polygonal epithelium. The lower surface has none."

Kölliker (1861, 166) studied the development of the cochlea, and concluded that ontogenetically the lamina reticularis, as well as Corti's membrane, are cuticular formations, both secreted by the cells of the epithelial ridge, beginning in the early stages of cochlear growth.

The cochlear canal begins to develop as a purely epithelial tube, and it shows on the floor which later on becomes converted into Corti's organ, three thickenings, one large and two smaller ones. The large epithelial ridge is covered by a structureless or, perhaps, finely striated membrane, the rudiment of Corti's membrane, and it is a cuticular product of the long epithelial cells.

Hensen (1863, 130) wrote: "The membrana Cortii is secreted in the embryo by a group of cells known as the Organon Köllikeri, which undergoes atrophy as the membrane increases in size, and whose function in consequence seems to be that of

secreting the tectorial membrane. It never leaves these cells, but lies upon them throughout life, except the anterior ends."

It is of a soft almost mucous consistency, withstands tearing with considerable force, and swells much in hydrochloric acid. The fibrillæ are separable, and there is probably an inter-fibrillar ground substance. In that portion of the lower face in contact with the teeth, one finds meshes of a network impressed on the surface. Corti's division of the membrane into four zones can, although they are usually present, be referred (H.) to external and secondary influences, and hence may be disregarded. The part lying on the teeth is relatively very thin. Not only is the thickness of the membrane subject to great variation, — depending on the height of the teeth or of the papilla or the sulcus epithelium, but also in the different parts of the same cochlear canal. At the hamulus and radix the membrane ends in a somewhat pointed and dentate manner corresponding to the end of the teeth and the papilla.

In breadth it increases as the hamulus is approached. The proximal edge lies in the line of origin of the memb. Reissneri. In the pig, however, it passes up onto this membrane a few cells breadth. The outer border was always found in adult human ears not to overlap or pass beyond the outer row of Corti's cells. It is at any rate certain that the membrane of Corti is fixed from the teeth over the lower wall of the sulcus, and outward from this lies free upon the rods of the lamina reticularis.

Loewenberg (1864, 185): The membrana Cortii shows three zones, — an inner, a middle, and an outer. The inner has no transverse striations and no network imprinted on its under surface. The middle zone has both. The striations really run obliquely to cross-section. They lie in several layers, and are arched over Corti's organ. Besides these I found a peculiar "accessory layer," which extended from the second third outward. This structure looked like a much perforated lamella, forming now and then a tissue of broad stripes. These stripes are nearly parallel to one another, and run in one direction, which nearly coincides with the border of the membrane. In sections, however, one sees that the perforations are in reality only thin places in the membrane, and the stripes are thickenings. Internally, this layer becomes very thin and its commencement very difficult to trace. Externally, it grows thicker and forms

a wedge-shaped portion in which one can distinguish a structureless mass inclosing an elongated portion that has the appearance of a number of capillary vessels in cross-section. Corti's membrane is related to the surrounding parts in such a manner that its inner and middle zones rest upon Huschke's elevation (promontory); it then applies itself to the epithelial thickening external to this and spreads out over Corti's organ, inserting finally on the upper process of the ligamentum spirale of the outer cochlear wall. By this means a canal is produced between the basilar membrane and Corti's membrane, and between this and Reissner's membrane another heretofore unknown canal, so that with the two scalæ there are four canals.

Henle (1866, 124): The cochlear canal is divided into two chambers by a membrane stretched across the canal parallel to the basilar membrane, from the labium vestibulare to the outer cochlear wall. This membrane — the membrana tectoria (M. Cortii) — is very delicate, but notwithstanding its thinness, firm and resistant and of a very peculiar brittleness and elasticity.

It is inserted on the outer wall between the insertion of the membrana basilaris and the stria vascularis. Three zones are distinguishable, the middle of which is composed of several layers of fine, somewhat bent fibres. The inner is structureless and perforated by many holes. The outer is composed of a very fine network made up of elongated meshes.

Middendorp (1868, 193): Corti's membrane is a cell secretion. It covers the crista sulcata from the inner angle of the membranous cochlea quite to the free border; from here it stretches across to the roof of the pillars of Corti, and ends in a narrow seam or line which is fastened to the first connecting members: a membrane with blood-vessels is never present. It is 1μ thick. It is a firm, elastic membrane.

Kölliker (1867, 167): The inner and outer hair cells all bear a brush of fine, stiff, short hairs, which are inserted on the top of the cell in a more or less semicircular line. The membrana tectoria was still considered to be a discrete structure having no organic relation to the auditory hairs.

Rosenberg (1868, 242): The largest portion of the epithelium of the lower wall of the developing cochlear canal is cov-

ered by a *cuticula*, the beginning of the membrane of Corti, which first appears on the median wall. It is quite thick for about half its breadth, and simply covers the outer supporting cells. Loewenberg's statement that Corti's membrane is inserted into the outer wall of the cochlear canal is incorrect.

Boettcher (1869, 31) gives a histological account of the development of Corti's organ, in which he describes the ontogenetic changes of this much-studied structure in detail as follows: —

Corti's membrane appears early in development as a thin, radiately striated skin (*Häutchen*) or membrane, lying close upon the epithelium of the lower wall of the cochlear tube, the thickest portion of which is near the inner edge. In the fully developed condition the membrane appears, when studied fresh, obliquely striated from within outward, diagonally upwards, *i.e.* towards the apex of the helix. It seems to be soft and yielding, but extremely elastic. At this time it is divisible into three zones. The inner zone begins at the inner angle of the cochlear canal and stretches across to the free border of the labium vestibulare. It is thin at its inner border, but grows thicker towards its outer edge. On its surface one finds even in newborn animals roundish or angular pits or grooves, which impressions are cell contours. In older individuals it is the teeth and ridges of Corti's organ which give the markings to the surface. The second zone is thick and has strong striation, and it reaches to the vicinity of the pillars of Corti. In the embryo it lies upon the large epithelial ridge. It grows thinner outwards, ending in fibrous prolongations that are continuous with (enter into connection with) the membrana reticularis, its whole outer border being divided up into ribs by means of vertical parallel incisions. Each rib sends downwards a fibrous, later divided process, a branch from which goes to the inner hair cell, whereas the other passes out over the three rows of Corti's cells and gives off to each an abruptly descending branch and then connects with the neighboring epithelial cells.

Corti's membrane is also in continuity by means of fibrous processes with the upper inner as well as with the outer descending hair cells. Whether these processes penetrate further into the cells cannot be determined. The hairs or rods of the auditory cells are consequently artifacts originating in the tear-

ing away of Corti's membrane. The third zone of the membrane is sharply marked off and begins with a hyaline border; then follows a network of fine trabeculæ with regular openings. The membrana tectoria is not, as Boettcher at first thought, united with the ligamentum spirale.

Boettcher correctly describes how the tectorial membrane develops with reference to the length of the cochlea. In pig embryos of 7 cm. length he found the membrane well developed in the second half of the first and in the first half of the second spiral turns, while both above and below this it gradually fades out, and is thus in harmony with the stage of development of the hair cells of these parts of the cochlea.

Winniwarter (1870, 292) says Corti's membrane shows three zones, the innermost thin, resting on the auditory ridge, very delicate, faintly striate, from occasional perforations presenting an imperfect netlike appearance and occasionally marked on its under surface by the outlines of epithelial cells which seem to be like those of the auditory ridge. The second zone begins at the end of the teeth, is striated diagonally from within and above, downwards and outwards, the striation being due to separable fibres. This zone ends outwardly in a border, rounded below, which is characterized by a hyaline edge. In the middle of this zone a dark line runs through the fibrous mass. The outer zone is composed of a network of structureless, anastomosing, hyaline meshes, the fibres of which arise from a hyaline edge. A more profusely branching plexus passes centrad over the surface of the membrana tectoria, extending far over the middle of the middle zone. The membrane is very resistant and elastic. It extends outwards certainly to the outer border of the three rows of the outer cells of Corti. The connection of the inner and outer pillars (*Stege und Saiten*) is a very firm one. There are about twenty-nine inner to thirty-eight outer.

Grimm (1870, 105) found the length of the hairs of the cristæ acusticæ to be 0.035 mm., while the cells were only 0.025 mm. high. The nerve fibre passes to base of cell; the axis cylinder pierces the wall, runs to the nucleus, on to the hair cap membrane, which it passes through, and ends in the base of the hair as a knob of stainable substance (black in osmic).

Hensen (1871, 129) corroborated Boettcher's observation that the inner and outer pillars of Corti are composed of fibres. He

regards the fibres passing out from the hair cells, or more strictly the cylinder cells of the large epithelial ridge, as artifacts, but believes most decidedly that the rods on the tops of the "hair cells" are genuine auditory hairs. He showed that the membrana Cortii cannot have the relations which Boettcher attributes to it, — is not so placed; that the third zone as a continuation of the membrane of Corti does not exist, for, on account of the migration of the pillar fibres, the pillars and the lamina reticularis would be shoved under the striated portion of the membrana tectoria. In the guinea-pig and rabbit he found in the several spiral turns of cochleæ treated with osmic acid that the outer boundary of Corti's membrane was exactly one-quarter of a cell breadth outside of the outermost hair cell. The third zone of Boettcher's is equivalent to the (co-extensive with the) fibrous network on the dorsal surface of the membrana tectoria as described by Loewenberg. The fibres of this zone cross the membrane fibres, and passing over onto the first zone appear to end in a sharp border.

This fibrous layer arises as Boettcher describes it, and always lies thrown back. The bars (*Balken*) from which it arises is the least elastic portion of Corti's membrane. As concerns his earlier view, that the membrana Cortii filled the sulcus spiralis during life, Hensen is unable to decide, and leaves the question open. He is uncertain whether the embryonic cells separate from the membrana Cortii with which they are so closely bound at first, but he has never seen the membrane with body large enough to fill the sulcus. Finally, Hensen describes a row of knobs on the lower surface of the membrane. It is always present in guinea-pig and rabbit, and is placed exactly above the inner hair cells.

Based on considerations of the anatomy and function of the cochlea, Hensen considers it certain that the nerve fibres end in the hair cells.

Hensen discovered in the outer cells a peculiar structure in the form of an oval capsule around which fibres were spirally coiled — they reminded him of sense buds (tactile corpuscles). Their normal position in the cell appeared to be directly underneath the cell cap. He found the capsules in other parts of the cell, but concluded they belonged in the top, and had been accidentally misplaced. As to their function, he favored the

view that they formed an end apparatus for the perception of pressure stimuli, in harmony with his view that the stiff hairs of the hair cells were bumped against or into the membrana tectoria, which rests upon them like a foreign body, by the vibrations of the membrana basilaris. In the case of the inner cell hairs they strike against the rows of knobs above described.

Hensen formerly thought the membrana Cortii was very soft and almost mucous in nature; he now thinks it to possess a resistance comparable to that of a pillow stuffed with feathers. Its stickiness is due to the fibrous net on its dorsal surface (Loewenberg's net), as well as to the fibrous nature of the membrane itself.

Gottstein (1872, 103): In man the membrana Cortii begins about the middle, between the attachment of the membrana Reissneri and the labium vestibulare. Within from this line is a continuous layer of epithel cells; but no trace of a tectorial membrane. The fibrous bodies of the pillars of Corti are composed of fibres which run into the basilar membrane. Protoplasmic remains have been found around their upper ends, and Waldeyer saw nuclei there in young animals.

The membrane of Corti is divided into three zones, and ends free in the neighborhood of the outermost hair cells. In the little epithelial ridge of the embryo there arises a triangular cell, which soon divides into two, in each of which a fibrous body appears, the first traces of the pillars of Corti.

The outer hair cells arise by the fusion (soldering) of two cells, an upper and a lower.

In animals the membrana tectoria begins near the line of insertion of Reissner's membrane; in man, further out (as above stated). The innermost zone reaches from this line to the labium vestibuli cristæ spiralis, thin and structureless; in man it is relatively thicker. The middle zone is separated from the first by a fine spiral line; it extends to the inner hair cells, and is especially thick and fibrous radially. The outer zone is separated from the middle by a slender hyaline spiral seam, and forms a fine-meshed network. The processes described by Boettcher, connecting hair cells and membrana tectoria, and the knobs on the lower surface of the membrana tectoria which Hensen saw, Gottstein could not find. Gottstein did not agree with Boettcher that the hairs occupy only a curved line on the

top of the cell, instead of taking in the whole cap, which latter view Gottstein adopted and figured the hair cells accordingly.

Retzius (1872, 238) found the cells of the cristæ and maculæ to be of two sorts, supporting cells and sense cells. The latter are flask-shaped, hair-bearing structures, which carry upon their thickened end plates tufts of hairs, ten to fifteen in number, and not infrequently even a larger number. These may be only the fibrils of a single large hair, and they are found of various lengths in maceration preparations. The auditory cells are directly continuous with the nerve fibres.

Nuel (1872, 207) gives an account of the tectorial membrane, but as it is reproduced in his later account, it will be given in a succeeding paragraph.

Boettcher (1872, 36): In the cat and the dog the Corti's pillars develop during the period shortly before and after birth. The hairs on the upper end of the hair cells are arranged in a curved line, not in a tuft, as Waldeyer thought.

He defends his views as to the nature of the membrana tectoria, viz. that the fibres of this plate are connected with the hair cells, and that the hairs of the latter are consequently artifacts.

In a young hare Boettcher found that the third zone (as Hensen found in rabbit) was formed entirely of a perforated membrane, which lies on the dorsal surface of the membrana tectoria propria and forms the inner part of the membrane, *i.e.* third zone. It is a genuine membrana fenestrata, and lies directly upon the cartilaginous spiral ridge. Further outward it lies over the striated portion, and reaches to the processes found on the outer border of the second zone. Adherent to these processes he found in the cat a row of fine fibres at very regular distances from each other, and a second row of similar ones nearer the ventral surface of the membrane. The membrane in hares is much thinner than in cats and dogs, and begins about the middle of the distance between the vestibular wall and the free border of the auditory teeth. The conditions in the rabbit and hare are unlike those in the dog and cat. In these latter there are fibres and outline figures upon the upper surface of the membrane.

These fibres are, so far as position is concerned, the equivalent of the fenestrated membrane of the rabbit. This is not

true of the third zone which unites with the border process further outward. Hensen's knobs are considered by Boettcher to be the remains of the connection of the membrana tectoria with the inner hair cells. Boettcher claims still in defending his earlier view that the membrana tectoria is tensely drawn in a radial direction, and calls attention to a homogeneous interfibrillar substance which lies between the isolable fibres. The membrane is elastic in a direction perpendicular to the course of the fibres and must be much more so in a radial direction. The only certain knowledge we have of nerve endings in the cochlea was gained from cross-sections in which the nerve fibres were seen to fuse with the inner hair cells. Of the longitudinal nerve fibres, he says: "Die longitudinalen Fasern werden nicht eher anerkannt werden, als sie auf den Durchschnitt demonstrirt sein werden. Das hat noch Niemand gethan, ja es hat an einen solchen sogar noch Niemand die Stelle angeben können, wo sie liegen." He calls attention to the possibility of confusing these spiral nerve fibres with the cell elements on the lower surface of membrana basilaris.

Hensen (1873, 33) concluded, after an examination of Boettcher's preparations, that his supposition was incorrect, that Loewenberg's reticulate lamella played a rôle in the formation of the membrana tectoria.

In Boettcher's preparations taken from embryos of the cat there extended from the membrana Cortii (which did not lie upon the membrana reticularis), out over the small ridge, a thin membranous plate. Below this membrane were fibrous structures, which were doubtless artifacts. This membrane, present in embryos, disappears later. The reticular membrane found over Corti's membrane (discovered first by Loewenberg) has nothing to do with the inner zone in guinea-pig and rabbit, but simply passes out over it, becomes very thin, and ends freely. Concerning the physical peculiarities of the membrana Cortii, Hensen does not agree with Boettcher that it is very elastic in radial direction, especially since we know nothing of its elasticity. He contradicts Boettcher's observations that the membrana tectoria is radially tensely stretched and that it contracts when broken loose.

After experiments instituted for the purpose, Hensen concludes that the consistency of the membrana tectoria lies

somewhere between that of contracted muscle and adipose tissues. It probably has the consistency of fresh brain tissue, and is much more resistant than the cells of the ridge, which have a consistency much like that of embryonic brain. Hensen concludes that he is certain that the longitudinal fibres are nerve fibres. He nevertheless admits that with the greatest care it is oftentimes impossible to tell nerve fibres from protoplasmic processes. He could not find Nuel's fibres.

Lavdowsky (1876, 178): The hair cells have the hairs always arranged in a *horseshoe* on the top of the cell. They are short, glassy bacilli, often rounded on the end, which in the fully grown animal are not organically connected with the membrane of Corti.

Lavdowsky found that some of the nerve fibres were not connected with ganglion cells, and that some of the nerves, after they had entered into the cochlear organ, end, not in the hair cells, but in the ordinary epithelium of the zona pectinata.

Corti's membrane begins near the root of Reissner's membrane as a very thin structure, but rapidly grows thicker. It extends with these relations through the whole of Corti's canal. It covers over the sulcus spiralis, Corti's arch, outer hair cells, and ends abruptly exactly over the last row of the outer hair cells, having decreased somewhat in thickness from its middle outward. Lavdowsky disagrees with Waldeyer that the membrana tectoria begins in mammals or in man midway between the root of Reissner's membrane and the labium vestibulare. Neither could he agree with Boettcher in this matter. In silver preparations Lavdowsky always found the point of origin very near Reissner's membrane. It can by no manner of means extend beyond the outer row of hair cells. As the membrane passes by the cells, it certainly does not enter into the kind of union with them figured by Boettcher, but simply applies itself closely to the hair cap of these cells.

"As regards structure, the first and last zones, *i.e.* the inner and outer, are homogeneous as I have found them, but I consider the homogeneity of the first zone different from other authors, since I find that the fibres of the middle zone narrow themselves inwards and not outwards; consequently the first zone is merely a modification of the middle one, whose fibres after narrowing down fuse with each other into a continuous

plate." He was not able to find any sort of cavities within the middle zone such as Waldeyer described. The figures on its lower surface, stripes, polygonal figures, are without doubt impressions of the surface of the structures on which it lies. The major part of the membrane of Corti is contained in the middle zone, which is fibrous. Its fibres are of very peculiar composition, long, for the most part undulating (in surface view), and very fine. They are especially soft, extensible, and very elastic in nature, so that the whole membrane has the nature of a soft, elastic mass.

Corti's membrane is, notwithstanding the contrary views of Hensen and Waldeyer, very elastic, and this peculiarity agrees well with its probable physiological function as a damping membrane. Its elasticity as a mass is due mainly to the inter-fibrillar substance, which Boettcher saw, and which Lavdowsky found was composed of inter-fibrillar granules. This substance easily swells up, and in so doing small vacuoles appear, in which condition Corti's membrane presents the appearance of a gelatinous, almost mucous mass. This substance is not found in the other parts of the membrane, *e.g.* in the outer zone. This zone is entirely homogeneous, still more elastic than the middle, which explains its more frequent distortion and displacement and rolling together. He could not accept Hensen's view as correct for the normal position of the membrane. He had nothing to add to Hensen's account of the hyaline border net nor the row of knobs.

Krause (1876) described the inner hair cells as bearing extremely finely pointed hairs. The outer hair cells differ from the inner in that they have an oval capsule entwined in a spiral nerve fibre, placed between the nucleus and hair-bearing cell cap.

Pritchard (1878, 217). In his account of the development of the organ of Corti, Pritchard says that, on the whole, Corti's pillars, the membrana reticularis, and the vertical trabeculæ have been developed out of the walls of the epithelial cells, while the *hair-bearing* and all other cells have developed from the contents of the original epithelial cells.

The membrana tectoria is a cuticular secretion of these cells.

Pritchard (1881, 216) described the auditory apparatus of *Ornithorhynchus platypus* and compared it with that of ordinary

birds and mammals. Our author concluded that the Platypus possesses a genuine organ of Corti, with two rows of the pillars of Corti; but the organ is in general not so well developed as in higher mammals, and greatly resembles the avian cochlea. The lagena with its sense organ is still present.

Nuel (1878, 206) accepts Boettcher's views, for the most part, with reference to the structure of the membrane of Corti, but does not agree with him in considering the hairs of the hair cells artifacts. He considered the membrane to be soft and non-elastic, and thought the polygonal depressions on its lower surface were derived from the membrana reticulata. The inner zone he found homogeneous, and is tunnelled by channels for the reception of the apices of habenula perforata. The membrana tectoria scarcely covers the membrana reticularis. Its outer zone is covered by a system of relatively large (coarse) anastomosing fibres. Nuel could not decide whether a considerable space was included between the membrane of Corti and the epithelium of the sulcus spiralis.

Although agreeing in the main with Boettcher regarding the structure of the membrane of Corti, Nuel adds a few new facts which his studies enable him to give beyond the former's account. The membrane of Corti is thrown like a plate or wing upon the habenula sulcata and the organ of Corti. It thus covers the habenula sulcata, the sulcus spiralis, and the organ of Corti in a radial direction.

In the spiral direction it extends throughout the whole length of the cochlear canal. It begins as a thin plate on the habenula sulcata, not far from the line of insertion of the Reissner's membrane, and in this region is composed of a homogeneous substance, and perforated by large holes which permit the passage of the processes of the habenula perforata, which are consequently not covered by the membrane. One might say that the membrane of Corti commences as a system of anastomosing trabeculæ lodged in the grooves of the habenula perforata.

At the extremity of the teeth of the first row, the membrane thickens considerably and passes out over the open space of the sulcus spiralis, from whence it passes on to the summit of the arch of Corti, but is there applied to the membrana reticularis.

At the apex of the organ of Corti it sustains a considerable

thinning, which approaches the plane of the reticular membrane. It extends scarcely beyond this membrane, but little is known concerning its true external termination. On its external border it is furnished with a system of quite large hyaline fibres, which by anastomosing form a sort of net, which for its beauty is not surpassed by the membrana reticularis and which Boettcher has well represented in his figures. This network reaches at least to the niveau of the external supporting cells, but its relation to the latter is not known. These trabeculæ of the outer border are in isolated membranes of Corti, usually bent inward over one or the other of its faces. Between the two systems of trabeculæ, internal and external, the membrana Cortii shows in a radial course a fibrous structure, fine but quite apparent. The constituent filaments, which are easily isolated in preparations, are undulating and lightly interlacing. The membrane tears readily in radial courses, following the direction of its constituent fibrillæ.

"Does there exist between the epithelium of the sulcus spiralis and the membrane of Corti a considerable open space? It is impossible for me to answer this question categorically. On the inferior face of this membrane one notices quite frequently polygonal depressions, which are in all probability produced by cellular elements. They may also correspond to the membrana reticularis."

According to Boettcher the membrane of Corti gives off branches of considerable size, which implant themselves upon the plateau of the cells of Corti and of the inner auditory cells. The rods carried by the cells are supposed to be remains of these processes which have been broken off in the preparation a little above the reticulate membrane. The description which we have given of these rods or hairs, and above all their regularity, renders, it seems to us, Boettcher's view inadmissible, at least as regards the significance of the rods.

The physical properties of the membrane of Corti merit all our attention. Hensen has announced, and I have many times verified the fact, that in the fresh state it is a soft substance, somewhat gelatinous and almost without elasticity. It takes and preserves all the shapes which one forces upon it with the instruments, and it rolls up without the least resistance. If we consider that such a pasty mass, as we may say, rests upon

the reticular membrane, it will allow of our making an hypothesis as to its physiological rôle. It there comes into contact with the rods of Corti's cells; quite probably the latter are plunged into its mass in a manner similar to the acoustic hairs which in the ampulla are thrust into the otoliths. The membrane of Corti will thus, very properly, annihilate the vibrations communicated to the acoustic cells (by the fibres of the basilar membrane probably), and thus play with respect to them the rôle of damper. The membrane itself is not capable of being put into vibration. It is a very poor resonator.

Embryological researches prove that the membrane of Corti is derived, not from the cells which constitute the embryonic acoustic papilla, but from the epithelium which covers the habenula perforata.

Retzius (1884, 237). In his extended monograph on the vertebrate ear, Retzius describes the membrana tectoria as extending from the insertion of Reissner's membrane to the outer hair cells. It is fixed to the tissue of the spiral blade, from its origin at the root of Reissner's membrane to inner edge of limbus lamina spiralis, but not structurally. This zone (the outer) is very thin, especially its inner border, growing thicker inwards. When the membrane is released from its position, which is readily done, the upper layer of the flat epithel of the limbus often pulls off with it, and gives rise to the polygonal areas or markings so often observed on its under surface.

Where the membrane leaves the free edge of the limbus it is marked by a fine line. From here it extends freely across the cochlear space, covering over the sulcus spiralis internus and the papilla acustica basilaris quite to its outer border — *i.e.* to the third row of hair cells — without, however, coming in contact with these cells.

The membrane closes in the relatively narrow space of the sulcus spiralis, which communicates with the other larger endolymphatic space only at the outer border of the membrane.

In this submembranous space the hairs of the auditory cells freely project. Whether they are in any way in contact with the membrane is extremely difficult to determine. In most preparations it appears as if they were not, since the lower surface of the membrane stands somewhat above them. In a few cases I saw it resting on the upper surface of the hairs. The

freely projecting membrane, however, scarcely allows of cross-section without dislocation, and the question is only to be decided by cross-sections. A good embedding method will probably answer it sometime.

On the under surface of the membrane in the rabbit there is no spiral ridge such as Hensen lately described. The membrane grows thicker rapidly after leaving the limbus, and the upper surface is convex in a radial direction.

In the middle spiral, the membrane is thickest at its outer border, and the upper and lower surfaces are here bound together by a relatively broad, convex edge plate. On the upper surface, somewhat within the edge, is a thick shining string or cord, that appears somewhat circular in cross-section, runs spirally, and is intimately bound to the surface. From it there passes out over the membrane a net of fine fibres running diagonally inwards, or really, with reference to the cochlear apex, from without and above downward and inward. The meshes of this fibre net of Loewenberg are oval fissures in its substance. In sections of the membrana tectoria this net appears as scattered granules over the surface of the membrane. This net does not extend further inward than to about the middle of the free zone; here the fibres become pointed and end themselves.

Of what is this membrane composed?

When one studies it fresh in aqueous humor, it is clear, transparent, gelatinous, firmly soft, somewhat elastic, so that it may be slightly stretched. When released, it contracts; when drawn too strongly, it splits diagonally and transversely, *i.e.* in the direction of the fibres of which it is composed. It appears while fresh to be striated diagonally from above and outward toward its inner and lower border, and under higher power it is seen to be made up of uncountable fibres which run in the given direction. Stained with fuchsin, the fibres appear sharper, rose-red, and they are separable by teasing. With gentle pressure the membrane is compressible, but returns to its normal shape on removal of pressure. Chromic and osmic acids make its substance firmer, but its composition out of fine fibres is just as distinct. Although these fibres stick closely to each other and are separable only with difficulty, one cannot distinguish a cement substance between them. But a minimum amount of such a substance is to be predicated as present

though not visible. The whole membrane is composed of such fibres, and they are apparent in radial sections, in which they are seen to run as arcs downward.

It has been proposed several times to distinguish zones in the membrane. In the rabbit, however, there are only two zones distinguishable, — the zone of the inner portion, fixed to the limbus spirale, and the free zone, both of which pass insensibly into one another, since the boundary between the two is confined to the stripe present on the lower surface. The two zones are also characterized by their different thicknesses.

Retzius (1884, 237): *Membrana tectoria* of the cat. This structure accompanies as usual the papilla basilaris from its base to the apex of the cochlea, *i.e.* throughout its entire length.

One can best distinguish two zones, an inner and an outer. These are bounded on the tympanal surface by the stripe, which is formed along the line of attachment of the membrane to the free edge of the labium vestibulare of the limbus spiralis. The outer zone extends from this free edge quite to, or perhaps somewhat beyond, the third row of hair cells. The inner zone extends from the free edge of the limbus to near the line of origin of the membrana Reissneri. The breadth of the inner zone of the membrana tectoria is different in the three spirals of the cochlea. It decreases in radial breadth gradually from the base to the apex, thereby decreasing the breadth of the whole structure. The membrane is consequently of different widths in the three spiral turns of the canal. The outer zone, however, gains in breadth from the base to the apex of the cochlea.

On the outer free zone of the tympanal surface of this membrane in the cat the striæ discovered by Hensen run in spiral direction. In perpendicular radial section it appears refractive, and, as Hensen stated, it lies almost directly over the row of inner hair cells. In the basal and spiral turn this *Hensen's ridge* lies nearer the edge of the limbus spiralis and is less distinct, and appears more or less serrated and broken up into papillæ, and is located about midway between the edge of the limbus (the bounding line between the two zones) and the outer edge of the membrane, consequently about the middle of the outer zone. In the apical spiral turn it appears again less sharply defined, and approaches nearer to the outer border of the mem-

brane. In several old cats I found Hensen's ridge as a very narrow stripe. Outside of Hensen's ridge, especially in the basal turn, one finds several projecting, irregular lines. Finally, one finds on the outer free border of the membrane a peculiar, refractive cord, which appears to represent the third zone of Boettcher. It is best developed in the basal turn, and is composed of parallel, refractive, and close-set fibres, whose direction is from within and below outwards and upwards (*i.e.* upwards towards the apex of the spire). These fibres seem to be collected into a single cord at the lower edge of the structure. In the middle turn this cord is single or only ribbed, and in the apical turn it is similarly constituted or else dissolved into branching fibres. On the vestibular surface of the membrane there are as a rule no fibrous structures present. Occasionally I saw, however, in old animals especially, in the middle turn, a faint indication of Loewenberg's net.

This face arches high above the edge of the limbus to fall again towards the outside. In the basal turn, consequent on the height of the lamina spiralis and the limbus, the direction of the membrane is towards the scala tympani. In the middle and apical turns, however, it is practically parallel with the basilar membrane. The tectorial membrane is thinner in the basal turn and thicker in the other two. The structure of the membrane is very similar to that of the rabbit. It shows in both zones an oblique striation, which runs from within and below outwards and upwards, which is due to the fine fibres of which it is composed. The course and other characters of these fibres, as well as the reactions and consistency of the entire membrane, agree with what has already been given for the rabbit.

Retzius (*ib.*) : The membrana tectoria is present in the cochlea of man, as in the rabbit and cat, as a flattened, band-shaped, soft, elastic structure, which runs along the whole of the papilla, is somewhat narrower in the basal turn, but broader in the middle and apical turns. Two zones are to be distinguished. The inner very thin zone is closely applied to the surface of the epithelium of the limbus spiralis, and is fastened by means of a thin, irregular, net-like cement-substance. The inner border of this zone does not reach quite to the root of the membrana Reissneri, but lies nearly midway between this and the edge of

the labium vestibulare. At this place one finds on the lower surface of the membrane a fine spiral stripe. The second zone of the stripe is suspended free over the sulcus spiralis internus and the papilla, rises towards the vestibular scala in the middle and apical turns, and thickens in the middle of its body, but remains thin in its free border, which here reaches scarcely to the outer row of hair cells. At the free border of the outer zone in the basal turn is found a thick, refractive marginal cord, which bends inward as it passes upwards. In the middle turn it forms a coarse-fibred, and in the apical turn a thin-fibred net, whose fibres project outwards free over the outermost hair cells. Occasionally one finds in the adult, especially in the apical turn, on the upper plates of the outermost Deiters's cells, the fibre piece, which is evidently a rudiment of the fibres which in embryonic life serve to attach the membrana tectoria.

Retzius did not find Loewenberg's net, or its equivalent, in man. About the middle of the lower (tympanal) surface of the membrane one finds Hensen's stripe. In the basal turn it lies somewhat nearer the inner border of the zone, in the middle and apical turns nearer the middle of this zone. In man this structure appears in the form of a somewhat refractive, relatively broad and flat plate with parallel contours, which lie over the inner hair cells, or more correctly immediately within this row. Both zones of the membrane are composed, as in the rabbit and cat, of innumerable extremely fine fibres, which withstand the action of acetic acid very well. Their course is from the base and within, outwards and upwards.

Retzius (1884, 237) says of Boettcher's observations in criticism of that observer's views: —

"Die membrana tectoria erstreckt sich mit dicker gewordner ausserer Zone bis über die gegend der äusseren Haarzellen; in der Spitzenwindung aber kaum bis zur zweiten Reihe, während ihre Fasern (*mcf.*) zwischen den mit frei ausragenden Haaren versehenen Haarzellenoberflächen zu den Phalangen der Deiterschen Zellen gehen. In der Mittel- und der Basalwindung sind diese Fasern abgebrochen und nur Reste von ihnen bewahrt; an der dritten Phalangenreihe sieht man helle Fasern (*mcf.*) aufragen, und nach oben-innen vom Membranrande nimmt man andere Partien der gleichsam zurückgeschnellten abgebrochenen Fasern wahr. Es ist diese Thatsache

interressant für das Verstehen der Boettcher'schen Angaben über den Zusammenhang der Membran mit den Haaren der Haarzellen; *mit diesen Haaren hat die Membran und ihre Fasern nichts zu thun.*" — II, p. 305, Pl. XXII, D, 1.

Barth (1889, 17) describes a homogeneous layer of substance separating the two fibrous layers of the membrana tectoria of the mammalian cochlea. He thinks that this membrane is much more important than usually supposed, and considers that it serves to fix the organ of Corti in its place.

The *membrana tectoria* of the mammalian ear has been described as a more or less gelatinous plate which, owing to its position overhanging the organ, is supposed to act as a damper upon the vibratory action of the sensory hairs.

The plate is continuous, and of course follows the windings of the cochlear organ. It is said to be firmly fixed (by adhesion, Retzius) to the limbus spiralis of the cochlea, and although easily removed from its position, not unfrequently brings away with it some of the pavement epithelium forming the covering of this portion of the limbus. The membrana tectoria has been described by Boettcher alone as possessing attachments to the organ of Corti itself, though more often so figured, and it is usually considered as a subsidiary structure, a mere cuticular secretion of the epithelial ridge known as the organ of Corti.

In the views which have been restated above, most of the investigators have described the minute structure of the membrane as distinctly fibrous, divided by certain inadequately known structural characters into inner and outer zones. There has been more general agreement upon these two points than upon any others. The striations of the body produced by its component fibres are continued, as I find, without hindrance through these zones. The fibrous striation of the organ is drawn outwards, toward the apex of the cochlea, and appears to pass from the inner edge (the so-called fixed edge) outward toward the outer side of the cochlear tube (free edge of the plate). We have been entirely in the dark as to the significance of this structure, its physiological function not having the least foundation in the actual structure of the organ. What is the phylogenetic origin of the tectorial membrane? This is a question which has proved up to date, under the prevailing views of its physiological importance, an insoluble puzzle.

When, however, we review the history of the controversy of the nature of the *cupula terminalis* and the gelatinous mass said to inclose the otoliths of the macula utriculi and macula sacculi, we find that the older view, according to which these structures were constant and normal organs of the internal ear, was forced to give way to the demonstration of their artificial nature brought by Hensen, and when we consider the view which I have endeavored to establish, viz. that the cochlear organ of the mammalian ear is morphologically but a transformed row of lateral line sense organs, each of which inherits the capacity to produce a structure in every way like the cupula terminalis, and when we examine the minute structure and relation of the parts of the *membrana tectoria* in this connection, I feel confident that it will be apparent to every one that the membrana tectoria of the mammalian ear is but a cupula terminalis-like structure produced by the gluing together of the hairs of the sensory cells of the organ of Corti and the breaking away of the whole from the cells which bear them, as in the case of the cupula hairs. This membrana tectoria, as it is found in ordinary microscopical preparations of the mammalian cochlea, is, then, an artifact produced by the use of reagents. In his later studies Retzius was converted to Hensen's view of the cupulæ terminales, and recognized two very definite forms in his own preparations which he called the osmium and Müllerian cupulæ respectively, since he was satisfied their peculiarities and distinguishing characters were due entirely to the reagents used. The effect of the following reagents are the only ones I have specially noted during my work, but any one who will test the matter and compare his results with the published figures will find the influence of reagents distinctly marked in the conceptions of the nature and relations of the membrana tectoria.

Hydrochloric acid swells the hairs, causing them to fuse and the boundaries to disappear. It shortens the length of the hairs correspondingly, so that in transverse sections the membrane is usually homogeneous and club-shaped when this reagent is used.

Nitric acid acts much in the same way as the hydrochloric, though it contracts the hairs much more strongly. This is especially true of the higher per cents (10–20) used in decal-

cifying. In combination with chromic and bichromic solutions it is very destructive of the fibres if left long in the solution.

Kleinenberg's salt picric and all aqueous picric solutions have little, if any, contracting effect on the hairs, and preserve the band in its normal relation, but render it easily separable from the ridge of Corti.

Solutions of copper salts above 1 % in strength contract the hairs too much, and cause rupture between the band and the hair cells. In weaker solutions, and especially in combination with 1 to 5 % of alcohol and of glycerine, the hairs are preserved in the normal condition.

Flemming's solution, if allowed to act on the entire embryo for a short time only, seems to have a good preservative effect on the hairs, and may be followed by alcohol and glycerine with advantage. Alcohol alone, unless cautiously employed during the first stage of the water-extracting process, causes ruptures and contractions in the hairs.

Chromic salts are useful if their action is not too violent or continued too long, for they readily bring about distortions in the hair band.

Essential oils almost invariably cause much distortion even of the carefully hardened hair band, and the paraffine bath usually adds something to the action of the clarifying medium.

Ether and strong alcohol, when acting for a protracted period, cause peculiar changes in the hair band, while

Aqueous solutions of gum arabic leave the hair band, as well as the organ of Corti, in very near their original form and relations.

The hairs of the organ of Corti while individually distinct, are so close together as to necessitate their cohesion into a long, relatively thin and narrow band. Its length in man is about 3.3 cm; in the cat, 2.3 cm.; in the rabbit, 1.5 cm. Its breadth in man is 0.5 mm.; in the ox, 0.48 mm.; and in the rabbit, 0.39 mm. The band is slightly broader in the middle than at either end, and somewhat broader at its upper than at its lower end.

In thickness it varies in different parts of cross-section, which tapers gradually from the origin of the component hairs from their cells to the inner free border, which lies on or above the limbus spiralis, where it fades away to a very thin edge. This edge, though composed of the extremely fine tips of the inner

hairs, appears very often in microscopic preparations under a low power to be homogeneous and glassy, but I have not yet seen a hair band whose inner edge was not resolvable into striation (the hairs) under adequate magnifying power. The densest part of the membrane is near the middle of its transverse section, and this coincides with the line of inner hair cells. The thickest part of the membrane is at the same time the most open, owing to the fact that it includes the origin of the hairs from all the sensory cells of Corti's organ, and of course the relatively large interspaces between the cell tops project up into the hair band, though continually narrowing until they fade out near the middle of the band. The band rises from the cochlear hair cells and with a gentle and graceful curve sweeps upwards and inwards, when, after reaching the height of its course, it slopes down to near the junction of the membrane of Reissner with the floor of the cochlear tube, where it ends. It declines on its inner face more gradually than it rises on its outer face. During life it is not attached to the limbus spiralis, as has been commonly believed, and, although I cannot say positively that it does not come in contact with this surface ever during life, I am sure that for the most part the hairs end free in the endolymph. The hair ends are to be seen on the surface of the band all along its course beyond the outer two-thirds of its breadth, projecting slightly above the surface of the band.

The band is composed of five (more or less) rows of bundles of hairs. Each bundle is the product of a single cell. The bundles remain distinct for a short part of their course, then apparently soon merging into a common structure. The spaces between the rows are greater than the spaces between the cells of the same row in the inner row of hair cells and the first row and, for the most part, the second row of outer hair cells, but often in the third and fourth rows of outer hair cells the interspaces between the neighboring cells of the same row are quite as great as the space between the rows. This circumstance renders the structure of this zone of the hair band looser and more irregular than the first-mentioned zones (Pl. XII).

The weakest part of the hair band is along the line of insertion of the hairs into the hair-cell caps, more strictly their origin therefrom. This condition is due mainly to the isolation

of the bundles, which throws greater strain upon a few hairs at a time, whereas in other parts of the band the cohesion of the elementary hairs and their practically even distribution in the band lends a strength to the whole structure such that a strain brought to bear upon any part of it, equal in area to a bundle of hairs rising from a cell, though sufficient to rupture the hair bundle, does not interrupt the continuity of the plate.

A further arrangement lending strength to the hair band is the crossing of the fibres; for the hairs from different rows of hair cells do not run parallel, but cross each other at varying angles. There are two main courses of hairs, an upper and a lower. The lower, from the inner hair cells, is more oblique to the radius than the upper, thicker layer, from the outer hair cells.

The readiness with which the hair band is torn away from its natural attachments and its frequent fixation to the spiral plate by its other edge, explain why this structure has so long been misunderstood, both in its make-up and in its purpose.

In transverse section the hair band is "clef"-shaped, the figure being much thicker at one end than at the other. There are two surfaces, two edges, and two ends. The morphologically dorsal surface has a convexity (that occurring in the thickened region) over the hair cells of the ridge of Corti, and this convexity may be said to be, in general, but a repetition in the hair band of the convexity of the ridge of Corti. In sloping downwards and inwards toward the root of Reissner's membrane, the surface of the band may form a shallow depression, in which case the usual "cleff"-form of the cross-section is attained; sometimes the hairs seem to run nearly straight to their ends, and then the section is ( ) comma-shaped. The lower surface follows these outlines in the main. The inner edge is excessively thin, and in bands which have been treated with reagents they usually present a glassy appearance, the longer the treatment with reagents or the more active the reaction, the greater the amount of changed tissue in the band, effected in all cases by the penetration of the reagent, which of course has made equal penetration over all the surface of the band, and caused equal chemical change in the fibres, but, owing to the thickness of the outer edge, the fibres in its central portion are unchanged and show through the more transparent parts, obscuring the

actual condition of the surface. On this account many observers have described the so-called inner zone of the membrana tectoria as homogeneous, glassy in transparency, and consequently of entirely different structure from the outer zone. However, as previously stated, even this inner edge when thus modified by reagents may be seen to be composed of fibres under proper manipulations of light and a sufficient magnifying power, unless it is completely melted down by the reagents.

The outer edge is thickest, and appears much thicker from the outside than it is in reality. The apparent edge when the band is in place is of course that part of its dorsal surface presented at right angles to the major part of this surface. The actual outer edge is that part of the structure composed of the basal ends of the long hairs, and its thickness equals the distance between the outer edge of the row of outer hair cells and the inner edge of the inner row of hair cells. When broken off from their respective rows the hairs are drawn closer together by capillary attraction, and the other forces at work altering the relations of the structures of the cochlea.

The two ends of the cochlear hair band are somewhat rounded, since the hairs at the extreme ends of the band are shorter than in any other part of the organ. The reason for this is the reduction in size and number of the hair cells at the ends of the organ of Corti, and, as we shall have occasion to notice further on, the membrana basilaris itself ends in rounded borders. The hair band is consequently thinner at its ends, and fades out quite suddenly at the limits of the hair-cell rows.

The individual hairs run entirely free and unsupported for their whole length, and are consequently completely bathed by the endolymph. Their extremely fine tips are specially free and well situated for the reception of the wave motions propagated through the endolymph. The space between the hairs is necessarily very small, and although difficult of measurement, I judge them to be less than the diameter of a hair in the middle, more massive part of the band. The hairs as they leave the top of the sensory cells are placed close together on the cell cap, but not always do they enter the cell cap with perfect regularity, which often appears concave from without inwards, though in many preparations the cap seems to be a simple plate

thickened and characteristically striate somewhat after the fashion of the "*Randsaum*" of the intestinal epithelial cells.

The number of hairs to a cell varies within considerable limits. The limits as I have found them up to the present are ten as a minimum and thirty as a maximum. Of the whole number of counts made twenty-five was the average. These figures are for the ox, pig, and rabbit. I am not sure that a variation in the size of the hairs is connected with the variation in number, nor do my observations suffice to determine whether the smaller cells bear the smaller number of hairs, and the larger cells the greater number of hairs. The hairs borne by the same cell appear to vary in size at their bases, but in objects so minute it is hazardous to draw conclusions from other than very extensive series of observations. The hairs themselves when seen free from the cell cap do not show noticeable variations in size, so that I am inclined to the opinion that the apparent variation in size, as seen on the cell cap, is due to optical conditions, *e.g.* such as the greater or less refraction of light by the hair bases depending upon their position.

In glycerine preparations of the cochlear sense organ of a young calf, and in similar ones of a new-born rabbit, the membrana tectoria is easily resolvable into its component layers. Two plates are specially easy to be distinguished, and they include between them the canal of Corti and the pillar cells, in that they arise from the outer and inner hair cells respectively and fuse together above the cochlear organ, but only after they have arched beyond the median line of the canal of Corti and its pillar cell rows.

Each plate as it passes down to the cells of the inner and outer hearing cells splits up into portions which end one in each sensory hair cell. The number of hairs passing into a cell I could not determine, but it is safe to say it is above eight. Owing, however, to the fact that the hairs appear to have the power of splitting up indefinitely, it is almost impossible to get accurate and trustworthy data of the number of hairs connected with a single cell.

The whole course of the individual hairs is very difficult to follow. In radial sections the hairs are invariably cut across, owing to their oblique course in the band, a single hair crossing obliquely a space measuring 0.013+ mm. Hairs do not ascend

or descend out of the layer from the cell row to which they belong, and in any given transverse section the hairs from the different rows appear to be of about equal length, so that the hairs of the outer row of sensory cells end on the upper surface before those of the next succeeding row by about the same interval that separates the rows of cells, and so for all the rows. In this manner the middle of the plate must necessarily be the thickest, while the inner edge of the band would be composed of only those hairs reaching inward from the inner row of cells.

Most previous authors have maintained, as I have shown in the historical introduction to this chapter, that the membrana tectoria was composed of isolable fibres held together by a common, more or less gelatinous matrix, the "Zwischensubstanz" or ground substance. I have examined many hair bands with the greatest care, using all the chemical and physical tests known to me, but have failed to detect a tissue, stuff, or deposit of any kind in the hair band between the hairs which was at all general in its occurrence or could possibly come under the head of a matrix for the fibres of the membrana tectoria as described by the older authors. According to my view of the nature of the hair band, and according to anatomical facts as I have found them, the hair band would not have a capillary matrix under normal conditions. It is true an excessive secretion of mucus in the ear might in a supposable case so coagulate as to imbed the hairs in a common mass, but I have never met with such a case, and I do not think mucus or any other albuminoids are produced inside the ear canals as they exist in living vertebrates, in sufficient quantities to give rise to such appearances in histological preparations.

The only conclusion admissible is that observers who have recorded the presence of such a matrix have had to do with pathological conditions, or post mortem changes, largely due perhaps to the reagents used.

It is a matter of importance as well as great interest to determine as nearly as may be the exact physical conditions of the parts of the nerve-end apparatus which are concerned in transmitting the physical energy, in the common acceptation of the term, into nerve energy.

Retzius, among others, and with more complete data than

most writers, has estimated the number of hair cells in the cochlear organ of man and other mammals. His figures, given in round numbers, are the following: —

The inner hair-cell row contains in man	3,500 cells.
" " " " " " " cat	2,600 "
" " " " " " " rabbit	1,600 "
The 4 outer hair-cell rows contain in man	12,000 "
" 3 " " " " " " cat	9,900 "
" 4 " " " " " " rabbit	6,200 "

As I have shown above, each hair cell bears a number of hairs which make up its bundle of percipient elements; and from the estimates which I have made up to the present time on the several species of domestic mammals mentioned before, the average number of hairs borne by the cells is twenty-five.

The inner hair-cell row in man would consequently support	85,000 auditory hairs.
The 4 outer hair-cell rows in man would consequently support	300,000 " "

According to Retzius's estimate, there are about 24,000 fibres in the tympanic layer of the basilar membrane in man's ear, while the cat possesses 15,700, and the rabbit 10,500.

These fibres were, according to the generally accepted Hensen-Helmholtz basilar membrane theory, the percipient elements *par excellence;* for on them, fixed as they are at both ends and supposedly tensely drawn, depended the transmission of the undulations of the endolymph to the hair cells. In place of these fibres of the basilar membrane I would substitute the 385,000 percipient capillary processes floating freely in the endolymph and connected directly with the sensory cell transmission apparatus, about which as yet we know so little, as the parts of Corti's organ which are sympathetically affected by sonorous waves entering the ear.

It is evident that the apparatus, which I have thus inadequately described, is far superior from a physical standpoint to the system of basilar membrane fibres for the work of picking up minute undulations, and the sequence of the physiological steps, which all our knowledge of sensory apparatuses lead us to accept as the normal condition, is maintained by this apparatus if it works as all investigators who have studied on the parent organs — the lateral line organs of fishes — suppose it does,

while the Hensen-Helmholtz theory introduces strange processes unknown elsewhere in animal physiology.

Retzius and most of the authors who had dealt with this topic before his time have maintained that the auditory hairs of the cochlear cells were not only short thick rods and quite stiff, but were inserted into the cell cap in a more or less crescentic line. Waldeyer and Gottstein, while agreeing with Retzius as to the length of the auditory rods or bacilli, do not agree with him as to the manner of insertion, claiming that the rods are certainly distributed over the entire surface of the cell end, and that with a nearly even spacing. They consider these rods to be distinct each for itself. When, however, we come to the auditory hairs of the other parts of the ear, all authors who mention the structure of the basal portion of the hairs describe a striated appearance due to fibrillæ, as Hensen claimed, and in this he was corroborated by Retzius.

These hair fibrillæ were found to number 18–20 per cell on cells of the ampullar sense organs of fishes, and a single fibrilla measured at its base 0.7μ in diameter; they were the constituent elements, as Retzius agreed, of *round* hairs. Their terminal ends were not described by these authors. Retzius has figured the hair cells (and several other authors have done the same, notably Hasse, Paul Meyer, and Hensen) from all sense organs of the ear other than the cochlear organ, as surmounted by a bundle of more or less broken fibrillæ, which he explains are the ultimate fibrillæ of the auditory hairs, but in every case attributes their individuality to the effect of reagents or mechanical injury. In Proteus the fibrillæ, or, at least, the striations indicative of their existence, were traced to near the tips of the auditory hairs. I think there can be no doubt as to the accuracy of these observations so far as they go, but the question arises, Do these fibrillæ remain compacted into bundles as is the case with the auditory hairs of the majority of the auditory sense organs, or are they separated during life? In the case of the organ of Corti, where the auditory cells are much more closely set than in the other sense organs, the fibrillæ or ultimate hairs certainly are independent of each other to a degree not found in preparations of the other sense hairs. Compare the cochlear hair cell from the opossum (Pl. VIII, Fig. 9) with the hair cells from the mocking-bird's ear (Pl. VI, Fig. 9).

A further question arises. Have we not here to do with a progression, a further differentiation, of the auditory hair in response to increased physiological demands? I think this

TABLE OF MEASUREMENTS OF THE LENGTH OF AUDITORY HAIRS IN VERTEBRATES.

Date.	Authority.	Publication. (List No.)	Animal.	Sense Organ.	Length of Hair in mm.	Number of Hairs to Cell.
1862	Schulze, F. E.	254, 255	Perca	Cristæ ac.	0.1108	
1881	Retzius, G.	236, 237	Myxine	" "	.009–.01	
"	"		Perca	" "	.055–.06	
"	"		"	Mac. utric.	.01	
"	"		Esox	" "	.0016–.02	
"	"		Raja	Cristæ ac. (cupula termin.)	.003–.0045	
"	"		Triton	Cristæ ac.	.035	
1884	"		Emys	" "	.06–.075	
"	"		"	All other organs	.018–.024	
"	"		Alligator	Cochlea	.02	
"	"		Pigeon	Cristæ ac.	.048–.054–.057	
"	"		"	Mac. utric. and sac.	.005	
"	"		"	Mag. neg.	.012–.015	
"	"		Frog	Mac. utric.	.011	
"	"		"	Lagena	.017	
"	"		Rabbit	Cristæ ac.	.03	
"	"		"	Cochlea	.005	
"	"		Cat	"	.005	
"	"		Cat embryo	"	.005	
"	"		Man	"	.008 (.005)	
1881	Hensen, J. V.	131, 132	Pleuronectes	Cristæ ac.	.19–.2 apparent	18–20
"	"		"	" "	.4 actual	
"	"		Frog	" "	.12 apparent	
"	Ayers, H.		"	" "	.2 actual	
1891	"		Mimus	Lagena	.34	8–28
"	"		Sheep	Cochlea	.5	
"	"		Pig	"	.5	
"	"		Cat	"	.55	
"	"		Rabbit	"	.38–.4	
"	"		Dog	"	.48	
"	"		Mouse	"	.5	
"	"		Rat	"	.5	
"	"		Guinea Pig	"	.45	average
"	"		Ox	"	.48–.5	25
"	"		Mimus	Cristæ ac.	.2 +	
"	"		Man	Cochlea	.4	25

question must be answered in the affirmative, and that each fibril acts independently, and as a unit; in other words, as an auditory hair, and not as a fibril of a hair, or one of a bundle of hairs. For I believe, though at present there is not sufficient morphological basis to give the view much weight, that each capillary fibril of the auditory cell of the human cochlea has independent connection with the brain through its own nucleo-neural filament and its own fibril of the transmitting nerve. If this were so, it would be possible for 770,000 separate impulses to reach the brain from the cochlear organs as the result of a single stimulus exciting the external air.

Loewenberg's net is a structure which was originally described by the investigator whose name it bears. It is apparently a network of fibres covering the membrana tectoria wholly or in part. It was found to be especially well developed on the outer surface of the tectorial membrane. For other histological details consult the historical account of the membrana tectoria in a preceding paragraph. This net, the membrana tectoria, with which it is intimately connected, and the membrana reticularis may be justly said to have constituted the three mysteries of cochlear anatomy, if one may be allowed to overlook those cochlear phantoms, the spiral, *i.e.* longitudinal, bundles of nerve fibrillæ of Deiters, Nuel, Retzius, and others.

Since I have frequently found this net, and since its nature was for a long time uncertain, I shall describe its ordinary appearance briefly as a preliminary to the account of its true nature, as deduced from a large series of nets. The net usually lies closely adherent to the surface of the membrana tectoria, and presents the appearance shown in Pl. II, Fig. 5. The coarser meshes are always nearest the inner edge of the hair band, while the coarser fibres are in the outer edge. These fibres or threads are very much like the fibres of the hair band in appearance and give the same physical and chemical reactions with few exceptions; *e.g.* the fibres of Loewenberg's net not unfrequently stain more deeply than the hairs of the hair band. Although the net is usually closely applied to the surface of the hair band in microscopical preparations, one often finds it more or less raised from this surface in fresh preparations, or it may be entirely absent from the organ. I have preparations of rat, rabbit, dog, pig, and opossum (Pl. XI, Fig. 2) which do not

show the slightest trace of Loewenberg's net, and they are perfect preparations, I may very safely say, so far as the preservation of the component parts of the organ of Corti is concerned. Chromic acid differentiates the net as well as any other reagent used. In aqueous humor, liquor amnii, and in weak solutions of copper salts the net is not formed. In Pl. IV, Fig. 7, is shown a section of the hair band of the Virginia opossum in which the net of Loewenberg appears as an appendage of the hair band attached to its outer edge. The sizes of the meshes in the most perfect specimens of the net are, as near as could be measured, the same as the upper ends of the cells of Corti's ridge beyond the last row of hair cells on the outside. The characters possessed by the net in one part of the cochlea may be found to vary from this condition in other parts of the cochlea, and such variation is not exceptional. The coarser, outer cords present, not infrequently, a striate appearance, which is due, I think, to the presence of auditory hairs. The net covers a variable area of the surface of the hair band, but never the entire surface, and usually about, or a little more than, half the surface. When all these facts are considered by themselves, we are left as much in the dark as to the nature of the net and the significance of its attachments as ever. An observation made quite recently on the *formation* of this membrane or network has made clear to me its nature and thrown some light on another structure, the membrana reticularis, which remains to be described. A perfectly fresh cochlea of the adult pig was opened in salt solution, to which was added, after five minutes, 1 per cent chromic acid, and the dissection proceeded with. As the preparation was being examined under the microscope (Hartnack, obj. 4, oc. 3), a thin film was seen to rise from the surface of the ridge of Corti outside the outer hair cells, *i.e.* beyond the edge of the hair band, which was still in place, and curve up over the hair band, the motion being around the line of fixation in the edge of the hair band as an axis. This film curved over onto and applied itself closely to the surface of the hair band. This film *did not* become *fixed* to the surface of the hair band, as an examination of a portion of the latter structure under a higher power conclusively proved, but remained entirely separated from it, except at the outer edge, where it seemed to pass structurally into the edge and to help

form the thickened border of the band. In structure this film was very like some of Loewenberg's nets that I had studied before, and when it was removed from the surface of the hair band no net was found below it. From this I concluded that the net of Loewenberg is only the loosened and displaced plate or film of cell caps of the ridge of Corti outside of the outer row of hair cells. There is nothing unusual in the process, as those might suppose who are not familiar with the old and highly reverenced mysteries of cochlear anatomy; for in the membrana reticularis, discovered and originally described by Kölliker, I believe in the first edition of his *Gewebelehre*, we have just such a film split off the tops of the cochlear cells *between* the hair cell of both rows and among the rows. Recall, for the moment, the relation of the parts of the organ of Corti as I have previously described them. A long ridge of more or less even surface, of unequal side slopes, with a crest of waving hairs fixed near the apex of the ridge. The surface of the ridge is continuous from side to side as a matter of course, and, since the body of the ridge is composed of columnar epithelial cells, the surface is made up of the mosaic of their ends, and as I have stated, this surface is quite smooth, the only inequalities being the thickened rims of the cell ends. The whole surface of the ridge is liable to artificial ecdysis under the influence of reagents, but owing to the insertion of the crest of auditory hairs, the whole surface cannot be removed intact.

Beginning on the outside in the bottom of the sulcus spiralis externus, let us follow the progress of such an artificial ecdysis. The cell-cap film is thinnest in the bottom of the sulcus externus, where the cells are smallest and least differentiated. It gradually thickens upwards as we ascend the slope. All over this free slope, which has no surface growths or projections, the film peels off freely, and is a continuous membrane until it reaches the outer row of hair cells. Since this film is more delicate and more exposed than the hair band, as regards its attachments, it is acted on more quickly, and, consequently, in preparations where the hair band is ultimately raised from the surface of the ridge of Corti, this thin film has already been displaced by the curling, distorting action of the reagent and taken its place upon the surface of the hair band as Loewenberg's net. As it curls upward the holes made in this sheet by the hair cells

slip like rings upwards over the basal ends of the bundles of hairs borne by each hair cell, so that when the hair band finally breaks loose from the top of the ridge, the film is firmly fixed by its inner edge to the outer edge of the hair band, and besides is usually closely applied to its surface, even if the action of the reagent has not caused a soldering of the structures at their points of contact. The fusion of the two structures does not always happen as the removable nets indicate.

The continuation of Loewenberg's net is the membrana reticularis, which cannot get out of place or become distorted, owing to the fact that it is perforated by holes, through which pass the hair bundles, which under the circumstances act like so many pegs to hold the membrana reticularis film in place, and, in fact, do materially aid in stretching the film tight and straight. On account of the coagulating and contracting action of such a reagent as chromic acid, the membrane is shrunk, but the firm fixation in the horizontal plane will not allow distortion of the plane surface or a shrinkage of the whole area of the membrane, so that the strain due to the shrinking action of the reagent serves to render tense the connecting bars of the reticulum of this so-called membrane. The remnant of the covering of the ridge of Corti, which lies upon the inside slope, extending into the bottom of the sulcus spiralis internus, is less frequently detached as it is more protected. It may be seen attached to the inner edge of the basal ends of the inner row of hair bundles of the hair band occasionally, but on account of its position and much smaller size, it is not so noticeable, and, so far as I can learn from the literature, has hitherto escaped notice.

I hope I have made it clear that there are in the living ear no such structures with physiological rôles as the membrana tectoria, membrana reticularis, and Loewenberg's net, and equally clear, I trust, that the structures of special value for the physiologist in the organ of Corti or mammalian cochlear organ are the hair-bearing cells, which stand on the crest of the ridge of Corti, and whose bodies are connected with the brain centres by the fibres of the cochlear nerve.

In closing the chapter on tectorial membranes I will quote the observations of Hasse (118, 1873), made in summing up his knowledge of the vertebrate ear after a long investigation of its structure. It will be evident that, although his observations

were made with the old ideas of their nature in mind, he has recorded no facts inconsistent with the account which I have given of the comparative anatomy of these structures.

"Ueber das auf der kuppelförmigen Wölbung der crista ausgebreitete Nervenepithel erstreckt sich nun, aber nicht über die Grenzen desselben hinaus und zuweilen bis an das Dach, immer aber bis zum oberen Drittel der Höhe der Ampullen emporragend, die membrana tectoria, die cupula terminalis (Lang), die ich auch an Embryonen von Säugern und Menschen nicht vermisst, eine cuticulare Bildung des embryonalen Nervenepithels der crista. Dieselbe ist eine muldenförmige ausgehöhlte, ausserordentlich leicht abhebbare, aber resistente Membran, deren Form ein Abdruck der kuppelförmigen Nervenepithelfläche der Gehörleisten ist. Sie zeigt sich zuweilen leicht streifig in der Längsaxe, jedoch ohne irgend welche faserige Struktur erkennen zu lassen. Diese Streifung ist der Ausdruck einer schichtweisen Absonderung der Membran. Die Dicke derselben ist entsprechend der hochsten Erhebung der Gehörleiste in der Mitte am beträchtlichsten, am geringsten dagegen an der Peripherie. In diese Membran ragen die Gehörhaare hinein und zwar befindet sich jede in einer tiefen Delle, deren Oeffnung an der ausgehöhlten, dem Nervenepithel aufliegenden Fläche sichtbar. Die Peripherie der Oeffnung ruht dem Basalsaume, der Circumferenz der Basis des Gehörhaares auf. Zwischen diesen weiten Oeffnungen der glockenförmigen Hohlräume oder Dellen der membrana tectoria finden sich dann kleinere, die rundliche, flache Vertiefungen anzeigen und sehr unregelmässig über die Fläche zerstreut sind. Diese rühren von den zuweilen etwas hervorragenden, keulenförmig verdickten, peripheren Enden der Isolationszellen her."

Page 79. "Abweichender verhält sich die membrana tectoria, die sich nur bei Myxine so verhält, wie an den Gehörleisten, verkalkt und als eine Otolithenplatte die gesammte Masse des Nervenepithels der macula acustica deckt, ohne anscheinend die Grenze desselben zu verlassen. Bei den übrigen Wirbelthieren nun, bei denen dieses namentlich in den niederen Formen bis zu den Vögeln empor der Fall ist, während bei diesen, den Säugern und den Menschen die deckende Masse sich wieder nur an den Bereich der macula hält, zeigt sie ein anderes histologisches Verhalten. Entwicklungsgeschichtlich betrachtet,

tritt sie auch hier in der Form einer von dem Nervenepithel und den Zellen der Umgebung abgesondert, mächtigen Cuticularmasse auf, allein sie beharrt nicht auf dieser Stufe, sondern, von den Neunangen angefangen, krystallisiren aus ihrem Inneren eine Menge von Kalkkrystallchen heraus, die bei den meisten Fischen sich zu einer zusammenhängenden Kalkmasse verbinden, und diese überwiegen schliesslich in einem so hohen Grade die Grundsubstanz, aus der sie sich bilden, dass dieselbe als eine mehr oder minder dünne, sackartige, den Otolithen oder die Otolithenmasse umhüllende Membran erscheint, die dann namentlich an der von der macula abgewandten Fläche ausserordentlich zart ist, so das nur in günstigen Fällen gelingt, dieselbe unversehrt zu erhalten und zu demonstriren. Ja es wäre möglich, dass dieselbe sogar bei den Fischen mit zusammenhängenden Otolithen an dieser Stelle verschwände."

"Der letzte, wesentliche Theil der macula ist nun eine membrana tectoria, wie wir sie sonst überall, sei es als solche, oder als Otolithensackmembran finden, und wir finden sie in einfacher Form bei den Reptilien und Vögeln, in complicirter dagegen bei den Säugern und den Menschen, bei denen sich als membrana Corti und reticularis bezeichnet wird. Die membrana tectoria der Schildkröten und Vögel, die wir zunächst gesondert betrachten wollen und die im Wesentlichen übereinstimmende Verhältnisse zeigen, deckt die ganze macula acustica, begiebt sich, wenigstens bei den Vögeln, nicht über den Bereich derselben hinaus gegen den dreieckigen Knorpel, das ligamentum spirale und hat demnach nichts mit den Stützzellen zu thun. Nur bei den Schildkröten scheint das der Fall zu sein, allein auch nur in geringer Ausdehnung. Wir finden, das dieselbe der ganzen Ausdehnung den auf der ausgehöhlten scala-media-Fläche des Nervenknorpels befindlichen Zahnzellen aufruht und sich in den sulcus spiralis hineinsenkt."

"Von diesen Zellen ruhren die grossen Eindrücke her, die wir an der ersten Zone der Unterfläche der membrana tectoria finden, und die Leiste, die bei den Vögeln dem sulcus entsprechend verläuft. Die Eindrücke der Zahnzellen rufen bei den Schildkröten ein reticuläres Aussehen hervor. Der übrige Theil der Membran, der gegen das Ende der macula immer dünner wird, zeigt auf der der macula zugewandten Fläche, wie die membrana tectoria der Ampullen und der Otolithensack-

membran, grössere und kleinere Oeffnungen, welche erstere in tiefe Dellen führen, die zur Aufnahme der Gehörhaare bestimmt sind, während die kleineren flachere Einsekungen zeigen, die das zuweilen keulenförmig verdickte Ende der Isolationszellen aufnehmen. Namentlich beim Frosche habe ich die glockenförmigen Hohlräume der membrana tectoria für die Gehörhaare ausgeprägt gesehen. Durch diese Kreisfiguren zeichnet sich bei den Schildkröten die zweite Zone, respektive die dritte Zone bei den Vögeln aus. Die ganze membrana tectoria ist eine cuticulare Abscheidung der Zahnzellen des Nervenknorpels, respektive der Zellen der macula acustica, und zeigt zuweilen eine Streifung als Ausdruck einer schichtweisen Ablagerung."

"Als solche ist auch die membrana tectoria der Menschen und Säuger anzusehen, die ebenfalls den Zahnzellen des limbus spiralis cartilagineus und, wie ich glaube, auch denen des sulcus spiralis anliegt, so dass es nicht zur Bildung eines canalis spiralis kommt. Immer finde ich an der abgehobenen Membran einen Wulst, wie der welcher sich bei den Vögeln in den sulcus spiralis erstreckt. Im übrigen zeigt die Membran auf dem Querschnitt wieder ein streifiges aussehen und breitet sich, allmählig dünner werdend, über die macula bis an die Stützzellen aus, erstreckt sich aber eben so wenig wie bei den Vögeln über diese hinüber. Auch hier finde ich die Eindrücke der Zahnzellen in netzförmigen Zeichnungen und die Haare der Hörzellen ragen an sie heran, allein sie deckt auch eine der macula acustica speciell angehörige und namentlich mit den peripheren Enden der Cortischen Zellen in Zusammenhang stehende Bildung, die membrana reticularis, die wohl ebenfalls als eine cuticulare Bildung, namentlich der Cortischen Zellen und der übrigen Isolationszellen, angesehen ist. Durch ihre Lücken ragen die Gehörhaare gegen die membrana tectoria. Die Annahme einer doppelten cuticularen Bildung, die im Wesentlichen denselben Zellen ihre Entstehung verdankt und von denen die eine sich nicht mit der anderen vereinigt — und von denem die membrana tectoria als die ältere, die reticularis als die jüngere anzusehen ist, ist um so weniger aus dem Wege liegend, wenn man den Befund, den ich einmal bei den Schildkröten gemacht, in Betracht zieht. Ich fand bei einer Chelonia midas eine Fortsetzung der Otolithensack membran des sac-

culus durch die ganze Schnecke sich erstrecken und die eigentliche membrana tectoria uberlagern, aber durchaus nicht an sie angeheftet so dass wir auch hier eine doppelte Absonderung der Zellen des Schneckenrohres annehmen müssen."

TABLE OF MEASUREMENTS OF SOME OF THE STRUCTURES COMPOSING THE MAMMALIAN COCHLEA.

(*Measurements given in mm.*)

	Rabbit. (R. A.)	Cat. (R. A.)	Cat Emb. (R.)	Pig. (A.)	Ox. (A.)	Dog. (A.)	Man. (A. R.)
Length D. cochlearis	16–17	25	—	—	—	—	35
" M. basilaris	14.5–16	23.5	—	—	—	—	33.5
Breadth tymp. wall D. c.	0.6	0.55	—	—	—	—	0.75
" vestib. " "	.42	—	—	—	—	—	.85
Height outer wall "	.33	—	—	—	—	—	.58
Breadth limb. spiralis	.2	.21	—	—	—	—	.24
" hair band	.33	.33	—	—	0.48	—	.41
" memb. basilaris	.41	.35	0.39	—	—	—	.36
Between pillar feet	.084 .104 .066	.102	.051 .09 .09	—	—	—	.09 .081 .048
Height of Corti's tunnel	.036	.046	.036	—	—	—	.045
Length of inner pillars	.06	.057	.057	—	—	—	.068
Vert. length of pap. basilaris at 3d row of outer hair cells	.09	.072	.065	—	—	—	.1
Length inner hair cells	.03	.03	.03	—	—	—	.024
" outer "	.039	.033	.035	—	—	—	.04
" hairs, inner hair cells	.30	.30	.29	0.5	.4	0.5	.40
" " outer "	.32	.32	.29	.5	.45	.5	.40
" outer pillars	.095	.09	.095	—	—	—	.103

THE TESTIMONY OF THE NERVE SUPPLY.

The vertebrate ear is then composed of canal organs and their canals; and since it existed at one time in its phylogenetic, as well as in its ontogenetic history in a superficial position, its nerves, like the other cranial nerves which supply the canal sense organs at the present day, must have been either (1) an entire cranial nerve or (2) branches of one or more such nerves. It can be shown, I think, that the ear is supplied by two distinct nerves which have widely different origins in the brain, and are in reality *branches from two nerves*, and so not a discrete cranial nerve, as has formerly been supposed to be the case. In our anatomies the auditory nerve is recognized, following the classification of Sömmering, as a distinct cranial nerve, the eighth in number of a series of twelve. However,

embryologists and comparative anatomists are familiar with the very intimate relation existing between the auditory and facial nerves, and many are inclined to consider the two, parts of a single cranial nerve. The majority of those holding such ideas probably favor the view that the auditory nerve is the dorsal sensory root of the nerve of which the facial is the ventral motor root.

No final conclusions can be drawn from the evidence disclosed by the investigations in this field alone. There are a few facts which stand out with clearness, however, and they tend to show how very intimate the connection is between the VII, VIII, and IX nerves.

I have shown above that the auditory vesicle is marked off into anterior and posterior portions very early in life; but we do not know of any facts which lead to the conclusion that the vertebrate ear was ever functional in the vesicular stage with *a single* sense organ. As soon as we can recognize the auditory nerve, it is made up of two diverging portions which are never related in their central connections, but arise from widely separated tracts. Each nerve root is provided with an independent ganglion applied to the two divisions of the auditory vesicle which show two sense organs, the maculæ utriculi and sacculi. There is no extensive anastomosis between the two roots of the auditory nerve.

They arise from separate tracts; they run in separate paths; they end in separate organs. Could there possibly be any completer evidence that these two nerves are distinct structures, and that the parts of the ear which they supply are simply associated organs of different pedigrees?

This conclusion is based on present anatomical conditions, and does not speculate on possible ancestral relations of the nerves.

If, on the one hand, the two roots of the auditory do not anastomose with each other, they do, on the other hand, enter into anastomosis, or more truly, perhaps, they retain their primitive anastomoses, with their parent branches. The anterior root or utricular nerve anostomoses with the facial nerve, while the posterior branch either runs entirely independent to its peripheral territory or anastomoses in some few Elasmobranch forms with the so-called anterior root of the ninth or glossopharyngeal nerve.

Although the ontogenetic evidence on this subject is not by any means as complete as the importance of the subject demands, since no special attention has been paid to the relation of the facial nerve to the auditory invagination, except by Kupffer, nor to the relations of the rest of the nerve supply of the ear at this stage of growth, which is usually considered the *whole* auditory nerve, there are certain facts which point to the conclusion that the auditory organ has arisen from the transformation of two originally distinct sense organs, which have been sunk below the surface in a common pit.

In order to adequately understand the relation of the auditory canal complex to its nerve supply, it will be necessary to examine three nerves usually classed as distinct cranial nerves, with respect to their central origin, their ganglionic connections, and their peripheral distribution; viz. the VII or facial, VIII or auditory, and the IX or glossopharyngeal. When we examine the knowledge of the external origin and distribution of these three nerves in the light of recent work, we find that so far as the auditory nerve is concerned the distinctly separate external relations are but reflections of central relations equally distinct and separate.

The innervation of the auditory sense organs in the Cyclostome fishes is manifestly a matter of importance, if, as I believe, the known representatives of the group are to be regarded as retaining, on the whole, ancestral conditions of structure.

In Myxine and Petromyzon we find the N. acusticus divided into two very distinct rami, — the anterior and posterior or utricular and saccular rami, respectively, — whose peripheral distribution is strictly confined to the chamber to which it runs. This is not only true of the Cyclostomes, but, with very slight changes, is true of all the Gnathostomata, and is consequently a fundamental fact whose full significance we are not yet in a position to fully appreciate.

According to Retzius, in the Hagfish (*Myxine glutinosa*) the auditory nerve arises from the brain, posterior to the origin of the V with two ganglion-bearing roots on either side. These ganglia are flattened bodies which lie close together, but are entirely separate structures. They give off several branches to the sense organs of the ear. From the larger, anterior ganglion two branches pass off to the crista ampullæ anterioris and one

to the anterior end of the macula acustica communis. From the smaller, posterior ganglion there is given off an anterior branch to the middle of the macula acustica communis, a posterior branch to the region between the middle and posterior end of the macula acustica communis, as well as to the crista acustica ampullæ posterioris. Both these branches are band-like and relatively small.

Of the nerve branches passing to the maculæ, that of the anterior ramus appears to be equivalent to the ramus recessus utriculi, so that the anterior end of the macula communis would be equivalent to the macula acustica recessus utriculi. The anterior branch of the posterior ramus is the equivalent of the ramulus sacculi, and its posterior branch, the ramulus lagenæ, so that the middle part of the macula communis equals the macula acustica sacculi, while its posterior end equals the papilla acustica lagenæ.

From the figures of the auditory nerve published by Ketel (160, 1872) and Retzius (237, 1881), the *smaller* posterior ganglion sends off two long, slender, flat branches, of which the anterior bifurcates and ends in the anterior part of the posterior half, of the macula utriculo-sacculi. The posterior branch of the posterior ramus bifurcates; the anterior branch turns inward and divides again and supplies the posterior portion of the posterior half of the macula utriculo-sacculi. The largest and most posterior branch runs direct to the posterior ampulla.

The nerves pierce the membranous cover of the ear by a row of holes running nearly in the long axis of the ear and below its middle. The following table gives in parallel columns the branches of the auditory nerve which I recognize in the Cyclostome ear and those given by Retzius. I maintain that a splitting of the trunk of a nerve supplying the auditory organs indicates the division of the sense organ supplied.

Ayers.	Retzius.
1. *r, a, a,*	= 1. *r, a, a.*
2. *r, e,*	
3. *r, m, u,*	= 2. *r, m, u.*
4. *r, r, u,*	
5. *r, l,*	= 3. *r, s.*
6. *r, s,*	= 4. *r, l.*
7. *r, ab,*	= 5. *r, a, p.*
8. *r, a, p,*	

In Petromyzon the rami anterior and posterior of the auditory nerve pass directly from the auditory foramen to the ampullæ, and as they approach the ampullar walls, they both divide into two branches each, which end in the cristæ acusticæ of the ampullæ.

The posterior ramus gives off a branch near the place where it separates from the anterior ramus, and this branch supplies the lagenar organ. The ramus anterior sends many fibres to the utricular sense organ and to the organ in the recessus utriculi.

The so-called ramus accessorius acustici accompanies the VIII through the auditory foramen and is closely bound up with it. According to Johannes Müller, the accessory branch is a part of the VII nerve, and from its distribution the facial nerve, as I find, supplies directly and independently two of the auditory sense organs and possibly also the ciliated epithelium, though there is no sufficient reason for doubting that the auditory proper may supply the ciliate epithelium in the parts of the ear to which it is distributed. It must not be forgotten, however, that the innervation of the ciliate epithelium has never been determined. It is usually stated that this unique lining of the Lamprey's auditory organ is innervated by the accessory nerve, and while I think this highly probable for the part of the ear within reach of this nerve, I believe the two branches of the auditory take part in the control of ciliate epithelium. This would call for motor fibres in the auditory nerve of Petromyzon, — not equivalent to musculo-motor nerves, perhaps, but none the less motor.

Ahlborn (1883, 1), p. 269, says of the auditory roots inside of the brain: "Alle die Elemente, welche in der beschriebenen Weise mit einander den Gehörnerven konstituiren, gelangen nun theils durch die obere theils durch die untere Wurzel aus dem Hirn, wie es in den einzelnen Fällen angegeben ist; dennoch ist die Trennung der beiden Wurzeln im Innern des Gehirns keine principielle, und gerade so wie die beiden Nervenkerne in einander übergehen, so treten auch einzelne Faserstränge des unteren Kernes mit der oberen Wurzel aus dem Hirn, und umgekehrt solche des oberen Kernes mit der unteren Wurzel. Beide Wurzeln vereinigen sich wieder in Ganglion Nervi acustici, durch dessen Vermittlung sie endlich in das Gehörorgan eingeführt werden."

Ahlborn (1884, 1), p. 300, says of the acustico-facial group in Petromyzon: "Die Acusticus-Facialis-Gruppe besitzt am Gehirn wie schon Wiedersheim zeigte drei übereinander dorsale Wurzeln, von denen die beiden unteren [anterior and posterior auditory rami] etwas näher zusammengerückt sind und den Acusticus ausmachen, während die obere Wurzel den Facialis bildet. Beide treten bekannter Weise in die Ohrkapsel ein, wo der Facialis das spinalartige Acusticus ganglion durchsetzt, um durch eine Oeffnung in der vorderen inneren Ecke der Kapsel auszutreten und das seitliche Horn des Ganglion Gasseri zu bilden, das er in lateraler Richtung wieder verlasst. Der Facialis steht mit dem Trigeminus so wie mit dem Vagus in enger peripherischer Verknüpfung."

Ahlborn says of the spinal group of the cranial nerves (*loc. cit.* p. 306): "Alle peripherischen sensiblen Bahnen dieser Nerven mit dem centralen Ursprungsgebiete des Acusticus in direkter oder indirekter Verbindung stehen, und das wir demnach in dem vordersten dorsalen Abschnitte der Medulla oblongata, welcher zur Seite der grössten Ausweitung der Fossa rhomboidalis liegt, das eigentliche Centrum aller dieser Nerven zu suchen haben." This central region of the spinal group of nerves is scarcely connected with the anterior region of the brain, and consequently, as Ahlborn states, this region must be pre-eminently one of reflex phenomena.

"Niemals wird es nach meiner ansicht, ohne willkürlichen Zwang gelingen, diesen Hirntheil und was aus ihm hervorgeht auf ein einfaches Rückenmarksschema zurückzuführen, und man wird sich endlich entschlissen müssen, so unbequem es auch sein mag, von der Anwendung des Bell'scher Gesetzs auf die hier in Frage kommender Nerven abzusehen.

"Man kann im Ursprugsgebeit der VIII–VII gruppe drei mehr oder weniger deutlich getrennte oder in einander übergehende Nervenkerne unterscheiden, von denen der obere am meisten gesondert erscheint und als Fascialiskerne zu bezeichnen ist, während die beiden unteren weniger bestimmt abgegrenzt sind und die beiden Wurzeln des Gehörnerven aus sich hervor gehen lassen."

With the Gnathostome condition there is in the simplest members of the group at our disposal for study already an increase from four to eight distinctly individual nerve branches.

The rami maculi and sacculi are further divided peripherally into numerous small branches, arranged in comate or pectinate order as the case may be.

This breaking up of these important nerve branches is in harmony with the growth of the sense organs to which they run. As Retzius has shown, the nerve branches to the maculæ acusticæ utriculi and sacculi are broken up into several or many branchlets almost as soon as they become distinct from the main trunk; nevertheless, they are to be considered together as forming a single branch. Retzius has not mentioned, however, that in some of the lower forms (Elasmobranchs) the nerve continues its *trunk* out to the distal portion of the sense organ it supplies, and gives off a series of branchlets all the way along. This mode of branching is to be considered the primitive one, since it agrees with the method followed by the nerves supplying long canals on the surface of the body, and the form described by Retzius is doubtless a secondary modification of it.

The form I have just described is produced in ontogeny by the rapid division of the sense organ in a linear direction and the breaking up of the nerve to supply the individual sense organs, which have thus become separated by short intervals from each other. This method of nerve branching is, so far as essentials are concerned, found in both the large, compound sense organs of the ear, viz. the macula utriculi and the cochlear organ.

Taking the groups serially, we find many interesting variations, which are, however, relatively unimportant from the morphological standpoint.

The auditory nerve in this group of fishes has the usual two branches which pass to the canal complexus at its inner anterior and inner posterior ends. The first-named branch is the ramus utricularis, and supplies the anterior division of canal organs. It divides into two main branches, the anterior ampullar and the utricular nerves. The former divides into two portions, one of which supplies the anterior canal sense organ, while the other passes on to that of the external canal. The second-named branch passes to the utricular sense organ and divides into as many discrete branchlets as there are sense organs in the group. The posterior branch is the ramus saccularis, and supplies the macula acustica sacculi and gives off a branch to

the posterior ampulla, which, by its division, has caused a division in the nerve, one twig of which supplies the crista acustica ampullæ posterioris, and another of which passes to the crista acustica abortiva division. The saccular ramulus, by a second division, has given rise to a ramulus lagenæ, which supplies the papilla acustica lagenæ, the parent of the cochlear organ.

As regards the relation of the auditory nerve to the facial and glossopharyngeal, we know the following facts. According to Stannius (268, 1849), the auditory nerve in *Raja batis* and *clavata*, in *Myliobatis aquila*, and in some few other forms, but by no means regularly among the Elasmobranchs, gives off a branch to the IX, which in turn sends a branch to the ampulla of the posterior canal.

In *Spinax acanthias* and *Carcharias glaucus* the ramus dorsalis of the glossopharyngeal nerve proves to be a very interesting branch, which arises from the nerve during its transit through the cartilaginous wall of the ear capsule. After leaving the IX, the ramus dorsalis curves dorsad behind the posterior canal, runs along on the top of the skull, underneath the muscles, until it reaches the region of the porus acusticus, where it breaks up into cutaneous branches to the sense organs of the canal communicating with the porus acusticus. This branch is not present in Batoid forms.

Scarpa (250, 1800) found the auditory nerve to be composed of two parts, a portio mollis, which he thought was a branch of the V, the VIII of later investigators, and a portio dura, the IX of more recent workers. The first of these supplied the anterior and external ampullæ and the anterior portion of the ear sac; the second part supplied the posterior ampullæ and occasionally the small otolithic sac, or what is now designated the sacculus. But this nerve always anastomosed with the anterior one before sending branches to the ear sense organs.

Weber (285, 1820) describes this anastomosis as made up of a branch of the nervus auditorius accessorius, which receives a small branch from the auditory proper and sends a relatively large one to the posterior ampulla.

Max Schultze (1858, 256) studied the anastomosis between the VIII and IX nerves, and concluded that there was certainly an interchange of fibres between the two nerves and not merely a contact of the two trunks.

As Allis (1889, 4) has shown (*loc. cit.* p. 513), "the facial nerve is the first one of the cranial nerves that takes any part in supplying the regular organs of the lateral canals."

"The R. ophthalmicus superficialis facialis supplies all the organs of the supra-orbital canal, *a separate branch being sent from the main nerve to* EACH GROUP *of organs* [italics mine]. This branch pierces the bony canal of the line immediately below the central organ of the group, and after entering the canal, sends a branch to each organ. This is the method of innervation in all the canals."

(P. 514.) "The R. buccalis facialis supplies the first thirteen organs of the infra-orbital line, and the R. oticus facialis the next three, making sixteen organs in all of this line supplied by the facial, or all those in front of the line of the opercular canal. *The remaining organs of the infra-orbital line are innervated by the glossopharyngeal and vagus.* This alone, or together with the branch to organ of supra-orbital, which leaves the main nerve close to it, probably represents the branch which, according to Wright (p. 513), supplies the organs of the transverse commissure in Mustelus. Wright is inclined to consider this most posterior of the dorsal twigs of the seventh in Mustelus as homologous with the ramus oticus in Ganoids and Teleosts."

"The sixteen infra-orbital organs supplied by the facial are separated by their innervation into four distinct groups. The . . . organs Nos. 14, 15, and 16 form the fourth group of the line, and vary somewhat in their method of innervation. Organs 15 and 16 are always supplied by branches of the R. oticus facialis. Organ 14 is sometimes supplied by a branch given off by the ramus oticus after it makes its exit on top of the cranium; but oftener, in specimens examined, it was innervated by a branch which left the nerve close to its origin, or even from the facial ganglion itself, near the root of the oticus, but a little in front of it."

(P. 516.) "Organ 17 is supplied by the dorsal branch of the glossopharyngeal. This branch arises by a separate root. . . . On this root a separate ganglion is formed, . . . and from it the dorsal nerve mentioned by Wright arises."

(P. 517.) "The remaining organs of the infra-orbital canal and those of the supra-temporal cross-commissure, as well as the organs of the lateral line, are all supplied by branches arising

from the ganglion formed on the root of the N. lineæ lateralis or from that nerve itself. The root of the N. lineæ lateralis receives its most anterior fibres at this age close to and a little above and behind the root of the N. acousticus."

"Piercing the membranes that separate the cranial cavity from the labyrinth, it runs directly backward, close to their outer surface and just above the posterior branch of the N. acusticus, in which there are numerous ganglion cells. It passes through the upper part of the main root of the glossopharyngeal, receiving there an important addition to its fibres, and, continuing backward immediately external to the origins of the anterior roots of the organs, it issues through the main foramen of that nerve."

In several instances the same nerve supplies sense organs which have had a divergent differentiation, as canal and pit organs.

The essential features of the innervation of the sense organs and their relation to the canals of the head region are clearly shown in Cut 25, which is reproduced from Fig. 49, Pl. XLII, of Allis's paper. The sense organs 16 and 17 of the infra-orbital system are neighbors in the now continuous canal formed by the union of the facial and glossopharyngeal sections of the canal system, which, as a comparison of Figs. 23–28, Pl. XXXVII, with the views of heads given in previous plates of Allis's paper and with the figure here produced, very clearly show, have grown together from independent sources. These figures also illustrate the interlocking of the territories supplied by independent nerves unusually well, for by their aid we are enabled to follow step by step the approach and final overlapping of neighboring territories. For example, the canal systems of the VII and IX nerves, although beginning their growth at entirely separated centres, grow towards each other and finally unite, the two systems opening out upon the surface at the junction by a common pore. (See stages of this growth on Pl. XXXVII, and the adult condition as illustrated in Cut 25.) As shown in cut, although the canals fuse to a continuous channel and the sense organs are approached nearer to each other, the nerves and organs are as distinctly separated as though the surface structures were entirely independent. The two nerves supplying this region of the common canal are

classed by morphologists as two distinct cranial nerves. As I have already stated, it is generally believed that these canal organs subserve a function akin to audition.

In the case of organs 16 and 17, their *centrally* distinct nerves run by *separate* paths and end peripherally in separate organs, having different pedigrees. The two organs, however, are inclosed in a *common canal*, which communicates with the surface by a *single* pore. Let us suppose these two organs with their incipient canals sunk below the surface of the head in a common depression, such as Allis describes for the organs themselves, early in development; the thickened plate of ectoderm out of which they were forming would represent not only the sensory epithelium, but also the epithelial lining of the *canals*, which would normally form were they to remain on the surface of the body. These canals would be represented by some growth after thus sinking below the surface. Thus, in the act of sinking, a common canal would arise, vesicular in shape, on account of the mechanical conditions of the deep involution. This common canal would open on the surface of the body by a pore, and this region of the canal, as the sense organs sank deeper into the head, would be drawn out into a tube. In thus going further below the surface of the head than usual, so far indeed that the connection with the surface canals would be broken, the sense organs would not lose their tendency to multiply as they normally multiplied on the surface of the body, and as they divided, their nerves would also be broken up into as many peripheral branchlets as there were sense organs. The increase in number of the organs, and especially their increase in functional importance, would lead to an alteration of the relation of the nerve branches supplying them. The two primary branches would become more and more independent of their parent trunks, the VII and IX, respectively, and would, on account of the compactness of the territory supplied by them, be drawn more and more together, until they apparently formed a single large nerve passing directly from the brain to the organ complex supplied by them.

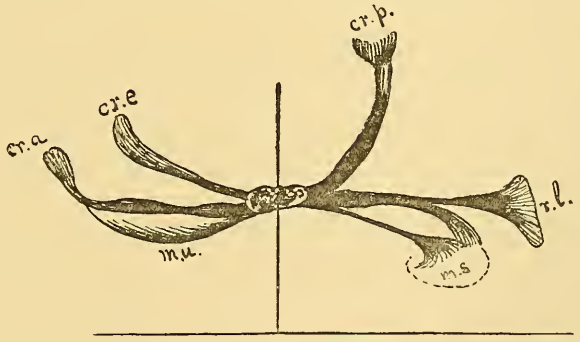
This process would influence the central origin, but in much less degree. However, as functional differentiation progressed, there would be a greater and greater separation from the parental ganglionic centres of those cells receiving the now special-

ized fibres from the sense organs of this now highly modified canal complex. *This same process occurs in the ontogeny of the auditory organ of the Elasmobranchs as the normal one.*

Thus we see that the conditions exist to-day in such forms as Teleosts and Ganoids, from which a second set of ear organs might readily be produced with a repetition of all the essential processes now occurring in the more ancestral Elasmobranchs, including the nerve supply, and the relative position of the organ with respect to the VII and IX nerves. Showing thus how it might again take place, aids us in comprehending how it has taken place in time past, and clears up many obscure points in the ontogenetic processes of existing Elasmobranchs, in so far as the auditory organ is concerned.

Goronowitsch found that both the dorsal branch of the VII and the anterior (dorsal) branch of the IX arose in common from the so-called dorso-lateral tract of Acipenser, which gives rise from its ventral portion to the auditory nerve, although a portion of its fibres arise from the posterior longitudinal tract.

He says (p. 511, *loc. cit.*): "Der Acusticus wird durch Fasern eines und desselben Charakters gebildet. Sie sind um etwas feiner als die Fasern des N. l. lateralis und beträchtlich dicker als die Fasern der dorsalen Wurzel des Facialis und des Trigeminus II." The nuclear connection Goronowitsch describes



Cut 12. — The branches of the auditory nerve of *Ostracion cornutus* and their distribution: *cr.a.*, *cr.p.*, *cr.e.*, the nerves of the three ampullar sense organs. *m.s.*, the nerve supply of the sacculus. *m.u.*, the nerve supply of the utriculus. *r.l.*, the ramulus lagenæ.

as follows: "Einen anderen Faserantheil bekommt der Nerv aus der Zellgruppe Az, welche ventralwärts vom Facialis (Radix

dorsalis) liegt," though the bundle of fibres from this source is relatively a small one. There is a distinct cerebellar connection.

According to Dr. Kuhn, after the auditory nerve in *Esox lucius* leaves the medulla, it runs a short distance in company with the facial, and then divides into two branches, the utricular and saccular. It is the utricular side of the auditory trunk that goes out with the facial, and this branch supplies the macula utriculi cristæ acusticæ anterioris and externalis. The saccular branch fuses with the glossopharyngeal for a short distance, and, according to F. E. Schulze, there is an exchange of fibres between them. The saccular branch supplies the macula sacculi, the papilla lagenæ, and the posterior canal organ crista acustica posterioris, with its offspring, the crista acustica abortiva.

According to Wright, *loc. cit.*, in Amiurus the dorsal branch of the facial arises in the tuberculum acusticum, from which also arises the anterior root of the IX.

The discrete external origin of the two branches of the VIII is most plainly seen in Teleosts, where the two roots are not infrequently separated by a considerable interspace. In Plagiostomes this matter of origin is much obscured, and, as above stated, the unified acoustic trunk may give off a branch to fuse with the glossopharyngeal nucleus. In some Cottids the nerve leaves the medulla by three branches, which have the following distribution in *Cottus scorpius*: —

1*st root.* This is the largest branch, and it issues from the medulla in close company with the motor root of the facial. It divides at once into several branches (three?) for the ampullæ of the anterior and horizontal semicircular canals and the utriculus.

2*d root.* This branch is very short, and runs straight from the medulla to the utriculus, receiving on its way a branch from the third root.

3*d root.* This is the saccular root, and almost immediately on leaving the medulla it gives off the anastomotic branch to the second root and then divides into two short branches, one of which supplies the sacculus, and the other ends in the crista of the posterior ampulla.

Stannius was in error in considering the third branch as forming a part of the (vestibular) utricular trunk of other forms.

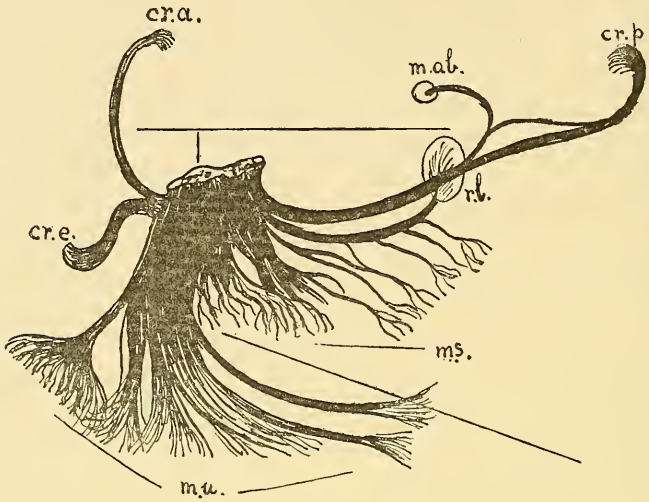
His error was the one commonly accepted at the present time; viz. that the three canals spring from the utriculus.

In studying the Cyprinoid brain, Mayser (1881, 191) found a very remarkable condition of things in the way of an intimate connection between the sense organ nerves and the auditory nerve. He says (*loc. cit.* p. 310): "Berücksichtigt man aber, dass die Nerven [*i.e.* lateral line nerves] aus dem Tuberculum acusticum, also einem zweifellosen Acusticuskern kommen, dass ihre Wurzel der eigentlichen (vorderen) Acusticuswurzel histologisch durchaus ähnlich ist, dass nach Stannius' Untersuchungen bipolare Ganglienzellen in die Fasern eingeschoben sind, wie es Fritsch im Anschluss an M. Schultze für den Stamm des Acusticus angiebt, so hat man gewiss alles Recht, hier zunächst an ein accessorisches Gehörorgan zu denken. Diese Vermuthung erhält eine bedeutende Stütze durch den eigenthümlichen histologischen Bau der Schleimkanäle, von welchen Leydig sagt 'Schon eine einfache vergleichende Beobachtung zwischen einem Bogengang des Gehörorgans mit seiner Ampulle und einer sogennanten Schleimröhre muss die wesentlich ähnlichen Beziehungen, die beide Organe mit einander gemein haben, anerkennen. Hier wie dort haben wir Röhren aus Bindegewebe bestehend mit zahlreichen Gefässen, und die von mir entdeckten Nervenknöpfchen entsprechen Vollkommen der Ausbreitung des Gehörnerven in der Ampulle.'

"Endlich spricht für die Auffassung der Schleimkanäle als Organe des Gehörsinns ihre Verbindung mit knöchernen Rinnen und Kanälen (am Schadel die ossa nasalia, infraorbitalia und Supratemporalia, Cuvier). Zwar ist Leydig der Ansicht, dieselben dienten bloss als 'Stützen und Schutz' für die Nervenausbreitung, allein man kann auch geltend machen, dass sie beim Aufenthalt im Wasser, also bei ausgeschlossener direkter Luftleitung die Schallleitung besser übernehmen als z. B. die sehr elastische Lederhaut. Ja, gerade diese Ansicht erklärt wenigstens einigermassen ungezwungen die von Leydig wiederholt ausgesprochene Bemerkung, dass man es hier mit einem speciell für den Wasseraufenthalt berechneten Sinnesorgan zu thun habe."

"*Somit spreche ich die Ansicht aus, dass die Schleimkänale der Fische nichts Anderes sind als ein weit über die Körproberfläche ausgebreitetes accessorisches Gehörorgan, von dem ich gerade*

nicht behaupten will, dass es Schallempfindungen zu vermitteln habe, dessen Funktion aber in den Bereich des zur Zeit noch unvollkommen erkannten Gehörsinns fallen wird." I think we may fairly conclude that Mayser was much nearer the full truth than he ever realized when he arrived at the conclusion above quoted.



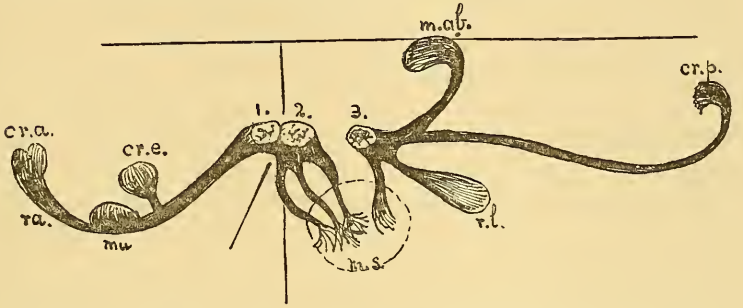
Cut 13.—The nerve supply of the ear of *Protopterus annectens* after Retzius. *cr.a.*, nerve of the anterior ampullar sense organ. *cr.p.*, nerve of the posterior ampullar sense organ. *cr.e.*, nerve of the external ampullar sense organ. *r.l.*, ramulus lagenæ. *m.s.*, nerve to the macula sacculi. *m.u.*, nerve supply of the macula utriculi.

Relying on the nerve supply, we find in Protopterus a condition of the macula neglecta with reference to its nerve supply which indicates that the whole of the sense organ originally budded off from the parent posterior canal organ has not left the parental home, so that the well-defined nerve ramulus neglectus is split about the middle of its course, one half passing to the separate *m. ab.* and the other apparently to the *cr. post.*, and there can be no doubt that the branchlet supplies a portion of the macula abortiva which has remained near the parent *organ group* to form a part of it. In many fishes the macula abortiva is divided into two very distinct sense organs, which receive each its own nerve supply; the macula abortiva is thus seen to be not merely a single sense organ, but a pair, the product of a bipartition. The primary macula neglecta does not always

carry away from the parent posterior canal organ sufficient energy to enable it to multiply.

The auditory nerve may be traced, according to Villy, in the larval *Rana temporaria*, long before the medulla is closed, from the neural ridge to the flat plate of thickened epithelial cells that later on is formed into the auditory vesicle.

In Tadpoles 11 mm. in length the auditory vesicle is completed, and the VIII nerve passing from the brain ends in contact with nearly the whole inner face of the vesicle, in the form of a ganglionic swelling. During this time "the auditory nerve is absolutely continuous with the facial nerve."



Cut 14.—The branches of the auditory nerve and their distribution in *Amphiuma means*, after Retzius. *cr.a.*, the nerve supply of the anterior ampullar organ. *cr.p.*, the nerve supply of the posterior ampullar organ. *cr.e.*, the nerve supply of the external ampullar organs. 1, 2, 3, the three trunks of the auditory nerve external to the brain. *m.ab.*, the nerve supply of the abortive ampullar sense organ. *r.l.*, the ramulus lagenæ of the posterior branch. *m.s.*, the nerve supply of the macula sacculi. *m.u.*, the nerve supply of the macula utriculi. *r.a.*, the anterior branch of the auditory nerve.

Strong (1890, 274) has stated (p. 600): "The facial of the Amphibia is divisible into two parts, very different from each other: A ventral part which persists in the higher vertebrates and corresponds, in part at least, to the facial of Mammalia; and a dorsal part representing in Chorophilus and Tadpoles the diminished remnant of a nerve, or group of nerves, which are much more important in the Urodela and remaining Ichthyopsida."

The dorsal branch of the VII, as defined by Strong, is given off immediately above the auditory; it soon divides into two branches, both of which are sensory. This branch of the VII is largest in Urodela and disappears entirely in the adult Rana

and Bufo. It will thus be seen that the facial may arise (apparent origin) dorsal or ventral to the VIII.

(P. 606.) "That the large sensory root of the facial, dorsal to the auditory (dorsal VII), together with the *anterior root of the glossopharyngeal*, form a distinct group by themselves, differentiated from the others by their internal origin and by the characters of their fibres, and belonging distinctly to the organs of the lateral canals.[1] It is possible that the auditory may have some relation to this system of nerves."

The so-called anterior root of the IX, according to Strong, usually arises some distance cephalad of the other roots, and also much more dorsally; its fibres are apparently all sensory, and its deep origin is not determined definitely, though its fibres go through the nuclei of the IX and X. "It is to be regarded as the lateral nerve, and, in respect to the origin of its fibres, their character and distribution, it agrees with the dorsal VII."

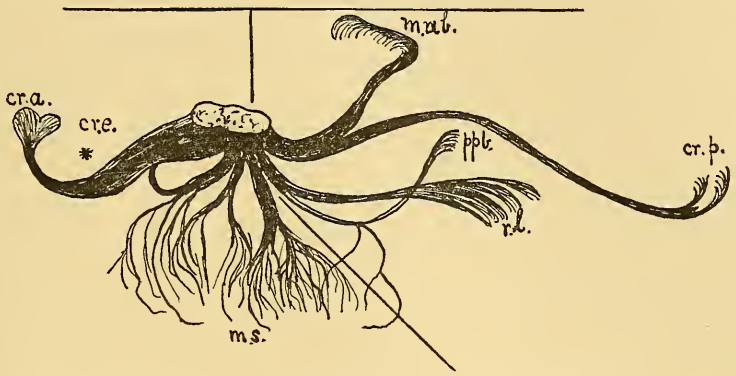
Strong concludes: "It is obvious that the connection of the dorsal VII with the lateral sense organs affords an explanation of its disappearance in adult Anura."

In Cryptobranchus, according to Osborn (*loc. cit.* p. 65, and Pl. V, Fig. 21), "the glossopharyngeus arises from four sources: 1. The fasciculus communis. 2. The large sensory nucleus. 3. A nucleus of doubtful motor cells. 4. A motor nucleus in the floor of the fourth ventricle. In Fig. 21 are shown the two nuclei belonging to the auditory nerve. One of these, the pale nucleus, lies dorsad and anterior to the other, which is placed more ventrally and internally, and is in close relation with the anterior glossopharyngeal nucleus."

Our author says (*loc. cit.* p. 66): "It is seen that whatever may prove to be the peripheral distribution of the fibres of the fasciculus communis and posterior longitudinal fasciculus, whether to the 7th or 8th, two facts remain: first, that the 8th arises ventral to the 7th, although a purely sensory nerve; second, it is inserted in the centre of the facial-trigeminal system, with no apparent homology in the arrangement of its nuclei to either." As regards the branching of the nerves on the utriculus and sacculus in the lower Amphibia, *e.g.* Proteus, it takes place much the same as has been described for Elasmobranchs, ex-

[1] See Recapitulation B.

cept that the group of branchlets supplying the sacculus leave the acoustic nerve as a trunk, almost immediately divide into



Cut 15.—The details of the nerve supply in *Menopoma allegheniensis*. *cr.a.*, *cr.p.*, *cr.e.*, the nerve branches of the anterior, posterior, and external ampullæ respectively. *m.ab.*, nerve to the crista acustica abortiva. *pp.b.*, ramulus papillæ basilaris. *m.s.*, the nerve supply of the macula sacculi. *m.u.*, the nerve supply of the macula utriculi.

two, and then each branch breaks up into a bundle of branchlets. Among the Anura, however, there appears a new branchlet from the cochlear nerve, which supplies the now discrete pars basilaris, the nerve having been split off from the lagenar branch in connection with the budding off of the pars basilaris.

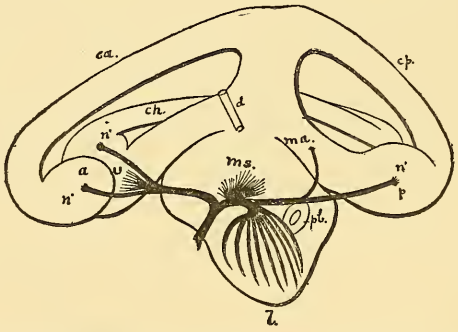
Among the Reptilia and Aves we notice a greater complication of the sense organ called pars basilaris, indeed of the whole cochlea, which involves the increase in size and the modification of the distribution of its nerve.

Here we begin to observe that fateful distortion of the ear chambers which has perhaps more than anything else retarded our progress in the knowledge of the significance of the parts of the ear and their actual relations to each other. The great development of the cochlea drags the posterior half downwards, backwards, and outwards in such a way as to give one the impression that the ear is divided primatively into superior and inferior portions. The division into anterior and posterior portions, which I have shown above to exist in the Cyclostomes and Elasmobranchs, obtains also in the Reptiles and Birds.

Among the higher Reptilia and the Birds the cochlear nerve has become the largest branch. The branchlet to the crista

abortiva in the Reptiles has grown noticeably smaller in connection with the regressive development of this sense organ, while among Birds the organ and its nerve are still further reduced.

The auditory ganglion, after the separation has taken place between it and the facial ganglion, divides, as Hoffmann states (*loc. cit.* p. 2015), "in zwei Theile, *einen vorderen und einen hinteren* [italics mine]. Der vordere Theil entlässt in der Gegend, wo der Facialisstamm abgeht, den Ramus anterior, s. vestibularis, der sich in drei Aeste theilt: 1) in einen Ast für die sagittale oder vordere Ampulle, der Ramus ampullæ anterioris; 2) in einen Ast für die horizontale oder äussere Ampulle, der Ramulus ampullæ externæ, und 3) in einen Ast für den Recessus utriculi, den Ramulus recessus utriculi. Der hintere Theil des Ganglion acustici rückt innerhalb des knorpeligen Labyrinths und bildet dort das sogenannte Ganglion cochleare. Von demselben entspringen: 1) ein Zweig, welcher sich nach dem Sacculus begiebt, der Ramus sacculi; 2) ein sehr starker Ast, der Ramus cochlearis, der nach der Cochlea geht und sich in einen Ramulus basilaris und in einen Ramulus lagenæ theilt; 3) ein Ast für die hintere oder frontale Ampulle, der Ramulus



Cut 16. — The right internal ear of the European Adder (*Tropidonotus natrix*), seen from the inside. Figure after Dr. Kuhn. This ear shows very distinctly the division into anterior and posterior chambers, especially in the arrangement of its sense organs.

a Anterior ampulla.
ca Anterior canal.
ch External canal.
cp Posterior canal.
d Ductus endolymphaticus.
l Lagena.
ma Macula acustica neglecta of Retzius.
ms Macula acustica sacculi.
n' Crista acustica ampullarum.
p Ampulla posterior.
pb Pars basilaris cochlea auct.
u Utriculus.

ampullæ frontalis, der den Ramulus neglectus abgibt für die Macula acustica neglecta an den Sinus utriculi posterior. Aus-

ser dem finde ich noch, dass von der dorsalen Wand des Ganglion cochleare ein sehr dünnes Zweigchen abgeht, welches sich, wie mir schien, nach der Wand des innerhalb des knorpeligen Labyrinths verlaufenden Theiles des Ductus endolymphaticus begiebt, später abortirt dasselbe wieder."

Kuhn's account of the innervation in adult Reptiles (Turtles and Ophidia) agrees with the later embryological evidence given by Hoffmann (*cf.* 172, 1882).

Retzius has called attention to the fact that Breschet (*loc. cit.* p. 89) had long ago (1833) correctly described the innervation of the parts of the human ear. Of late years, however, anatomists have neglected Breschet's investigations and adopted the erroneous statement that the three ampullæ of the semicircular canals are supplied by the vestibular (*i.e.* utricular) branch of the auditory nerve. Retzius was led to renewed investigations on this point by finding that all other vertebrates than the Mammalia, although agreeing among themselves as to the innervation of the parts of the internal ear, differed in this one thing from the mammals. The results of his studies form another contribution toward the demonstration of the intimate genetic relationship of all vertebrates above Amphioxus.

As we have just shown, the Ganoids, Dipnoids, Teleosts, Amphibia, and all the Reptilia and Birds agree in essential particulars with the Elasmobranchs; and many forms from the larger groups, and several from each of the smaller groups, have been accurately studied in this respect. The relations of the parts in man and the Mammalia had long been in a confused state. We now know, thanks to the painstaking and skilful investigations of Retzius, that man forms no exception to the general law governing the development of the ear in other animals, and that he has no parts not represented in Elasmobranchs in some condition. The distinctive features of the human ear as a type of the mammalian class is the great differentiation of the cochlear region with the consequent distortion and more complete separation of the parts of the canal complex. It is with regret that one finds these misleading errors diligently perpetuated in our text-books of science. In revising the chapters on the nervous system for the fifth edition of his text-book of Physiology, Foster has retained the erroneous account of the innervation of the auditory organ, on which he bases certain

conclusions with reference to the functions of parts of the ear which are entirely untenable, owing to the false anatomical premises. He says (*loc. cit.* p. 957): "When we come to study the ear we shall find that *one division of the auditory nerve is distributed to the cochlea alone*, and is called the nervus cochlearis, the *rest of the nerve* being distributed to the utricle saccule and semicircular canals as *the nervus vestibularis*" [italics mine]. As we shall see, there are reasons for thinking that the vestibular nerve carries up to the brain from the semicircular canals impulses other than those, or besides those, which give rise to the sensations of sound, whereas (he continues) the cochlear nerve appears to be exclusively concerned in hearing; and in some structural details these two divisions of the auditory nerve differ from each other. Hence it is important to note that according to careful investigations the cochlear nerve is the continuation of the dorsal root, and the vestibular nerve the continuation of the ventral root.

The latter statement is correct when the previous error is corrected, for that the *cochlear nerve* supplies the *cochlea*, the *sacculus*, and the *posterior ampulla* in the *human subject is a fact beyond dispute*, and since physiologists lay such weight of speculation on the nerve relations, it is desirable that the anatomical basis should be as exact as possible.

In his account of a 16 mm. sheep embryo, Boettcher, in his extensive monograph (31, 1869), p. 15, says: "Untersucht man die mehr nach vorn gelegenen Querschnitte so findet man noch eine zweite beträchtliche Gruppe von Ganglienzellen (*G'*), welche durch ein starkes Bündel Nervenfasern mit dem Nachhirn in Verbindung stehen (Fig. 9, *N*). Dieses Ganglion liegt dem mittlern Theil der Labyrinthblase an und befindet sich, wie bemerkt, vor dem Ganglion cochleare. Dasselbe gehört unzweifelhaft, wie später genauer erörtert werden soll, zum grossen Theil dem Nervus vestibuli an; inwieweit der facialis mit seiner ganglionalen Anschwellung dabei betheiligt ist, lässt sich in diesem Entwicklungsstadium nicht scharf entscheiden; es scheint, dass eine Abgrenzung beider um diese Zeit überhaupt nicht möglich ist."

In an embryo 2.0 cm. long Boettcher found the following condition of the nerve apparatus (*loc. cit.*): "Ausserdem bilden sie eine continuirliche Reihe, welche mit der Hauptmasse des

Ganglion cochleare zusammenhängt. Dieses findet sich weiter nach vorn an der Spitze des Schneckenkanals angehäuft und tritt auch hier hart an denselben heran. Diese Hauptmasse des Ganglions steht, wie weiter nach vorn fallenden Querschnitte lehren, ohne scharfe Grenze in Zusammenhang mit einer andern Nervenzellengruppe, welche, dem mittlern Theil der Ohrblase anliegend, den grössten Theil des Raumes zwischen dieser und dem Hirn ausfüllt und letzterem nach oben zu Fasern zusendet.

"Diese nervösen Bestandtheile gehören zum Theil dem Fascialis, zum Theil dem N. Acusticus an; eine scharfe Scheidung der einzelnen Faserbündel sowie der ihnen zugehörigen Ganglien tritt erst später ein."

The acoustic nerve is composed of loosely bound nerve bundles, which may be separated in the nerve trunk (and do farther on actually separate) into two branches, the ramus anterior and ramus posterior. The first lies in front and above and runs beside, and later outside of and below the facial, passing outwards, forwards, and upwards to enter the utricular chamber through the so-called macula cribrosa superior.

The ramus posterior passes outwards, backwards, and downwards, and divides into two main portions, (*a*) ramulus cochlearis and (*b*) ramulus sacculi, which gives off the elongated ramulus ampullæ posterioris.

There is not the slightest trace of a ramulus maculæ neglectæ, though there is an anastomotic branch given off from the ramulus ampullæ posterioris to the *ramus anterioris*, a condition of things of frequent occurrence in vertebrates. If the macula neglecta did occur, it would in all probability be found on the floor of the posterior ampulla. It is needless to say that the ramulus cochlearis forms the greater portion of the posterior branch. The number of discrete divisions of the ramulus basilaris has reached in the human ear at least 100 to 125.

In a short paper on the histology of the medulla, Kölliker has recently (163, 1891) called attention to the relation of the sensory nerves to the brain first established by His. He says (*loc. cit.*): "Alle sensiblen und centripetal leitenden Elemente des X, IX, VII, und V Nerven, sowie des Acusticus entspringen nicht im Gehirn, vielmehr sind die Ansammlungen grauer Substanz, die man bisher als Kerne dieser Nerven betrachtete, Endstationen derselben, die ich schon in einer früheren Arbeit

mit His als Endkerne bezeichnete. Die wirklichen Ursprünge dieser Nerven liegen wie His zuerst nachwies, in den Ganglien derselben, ausserhalb des Gehirns (Ganglion jugulare und petrosum, Ganglion nervi Cochleare et vestibuli, Ganglion geniculi, G. Gasseri)." This constitutes another important proof of the great similarity existing between the auditory organ and the other sensory structures of the surface of the head supplied by the nerves mentioned above, and proves conclusively that so far as innervation is concerned they all belong in the same category.

Before entering into a tabulation of the central relations of the branches of the auditory nerve and the relations of the roots outside of the brain proximal of the superficial ganglia, let us examine some of the features of the development as given by His, Jr. (*loc. cit.* p. 5): "Die Ganglienanlage besteht also in diesem Stadium der Entwickelung [3½–4 weeks] aus einem äusserlich ungegliederten Complexe von Zellen, in welchem aber bereits mehrere Abtheilungen sich deutlich erkennen lassen:

"1. Die mediale Abtheilung, mit der lateralen Acusticus Wurzel und den in ihr aufsteigenden Zellen.

"2. Die laterale Abtheilung, mit der medialen Wurzel.

"3. Die ventrale Abtheilung, in Verbindung mit dem Nervus facialis.

"Peripher von dieser Ganglienanlage ist ein Stamm des Acusticus nicht zu erkennen; dieselbe liegt vielmehr der vorderen Wand der Gehörblase (mit Ausnahme des Aquæductus vestibuli) auf das Engste an; *nirgend ist eine Mesodermschicht zwischen beide Gebilde eingelagert* [italics mine].

"*Es gehen nun aus dieser vorderen Wand alle diejenigen Theile des Labyrinthes hervor, welche später Nervenendstellen erhalten,* und es erhellt daraus, dass alle diese Theile zu einer gewissen Zeit zum Ganglion in directer Beziehung stehen. *Ausgenommen ist allein die Ampulle des hinteren Bogenganges: diese erhält ihre Innervation erst sehr viel später* [italics mine]. Obwohl ich meine Aufmerksamkeit auf diesen Punkt richtete, ist es mir nicht gelungen bei Embryonen unter 6 Wochen einen Ast zur hinteren Ampulle aufzufinden. Mit dieser einzigen Ausnahme ist aber durch die beschriebene Anordnung die Ausbreitung der Nerven auf die verschiedenen Theile des Labyrinthes in voraus bestimmt."

A TABLE OF THE MAIN RELATIONS OF THE VIII IN MAN.

In Man the VIII nerve { Leaves the brain from the groove between the pons and restiform body as two cords containing between them from one to several small nerves, the portio intermedia Wrisbergii.

Ramus Anterior or Utricular Nerve.	VENTRAL, *anterior*, median, superior.	The nucleus of this nerve lies medial from the corpus restiforme; its fibres ascend to the cerebellum (Bechterew); in part it runs into the lateral nucleus Gegenbaur. It is connected with the nl. of Deiters, and the gang. geniculi (portio intermedia). It passes into the brain along the ventral face of the corpora restiformia, reaches further dorsad and caudad than the dorsal root. The portio intermedia passes out of the brain a little in front of the ventral root: it arises in the accessory nucleus. This root passes to the median side of the restiform body, between it and the ascending root of V, and so reaches the lateral[1] (division of the) nucleus among the large cells of which most of its fibres end: the others are continued on to the cerebellum along with the fibres of the restiform body; possibly these fibres run into cells of the nucleus before passing on to the cerebellum.
Portio Intermedia, *Wrisbergii, N. VIII.*		The portio intermedia is a sensory facial branch homodynamous with the utricular branch, and both belong to the VII.
Ramus Posterior, or Saccular Nerve.	DORSAL, *posterior*, lateral, inferior, inner, principal, central.	The nucleus of this nerve lies laterad from the corpus restiforme. None of these fibres have direct connections with the cerebellum. Most of the fibres end in the nucleus inferior (*i.e.* accessorius) which is connected with the trapezoid body (Bechterew). This nl. is intimately connected with the nl. of the IX. As it enters the brain it winds round to the dorsal surface of the corpora restiformia, reaches further ventrad and cephalad than the ventral root. The major portion of the dorsal root ends in the accessory[2] nucleus and in the nuclear mass just dorsad of it (tuberculum acusticum), from whence it curves around the corpora restiformia and ends partly in the median nucleus after causing the striæ acusticæ. The connection with the median nucleus is an association relation. The anterior nucleus overlaps that of the VII. The posterior nucleus overlaps that of the IX. The saccular nerve is a branch of the glossopharyngeus.

[1] This is the dorsal nucleus of Edinger.
[2] This is the ventral nucleus of Edinger.

According to Hoffmann and Rauber, the anterior portion of the nucleus of the IX nerve, *i.e.* the very anterior end of the glossopharyngeus nucleus, is regarded by Duval and others as the nucleus of origin of the chorda tympani and of the portio intermedia Wrisbergii of the auditory nerve; however, the mass of evidence seems to favor the view of a closer connection with the anterior root and the facial than with the posterior root and the glossopharyngeal.

C. Sense Organs.

Development in Amia according to Allis.
Development in Elasmobranchs in connection with the ear organ.
Development in bony Fishes.
Development in Amphibia.
Development in the Sauropsida and Mammalia.
Views previously held of the function of these sense organs and of their relation to the ear, both analogical and homological.

The Development of the Sense Organs in Amia.

A knowledge of the development of the lateral line sense organs (*e.g.* as it has been worked out in Ganoids) enables us to understand the development of the internal ear, and is absolutely essential to such understanding. I give the account of the development of these superficial organs in Amia in Allis's own words. He says (*loc. cit.* p. 523 *et seq.*): "The inclosing of the lateral canals and the formation of the ninety-three normal primary pores and tubes is essentially a simple and regular process, but in most parts of the head marked abbreviations take place, which greatly obscure it. Where the process is *regularly and fully carried out, the canals arise in separate sections, each of which contains a single sense organ, and hence corresponds to the part between two primary tubes in the developed canal* [italics mine].

"In young Amia, in which the canals have not yet begun to develop, the organs of the lateral system, still below the surface, appear as whitish spots, with indistinct outlines, strung along more or less continuous whitish lines. These lines mark general and extensive surface depressions. *After a developing canal organ has reached the surface at the bottom of one of these depressions, it begins to sink, carrying with it the surrounding tissues, thus forming a small pit, at the bottom of which the organ lies* [italics mine]. A series of changes now begin, which, on an exaggerated scale, are a repetition of those which lead to

the division of a pore. *Lips grow upward and inward from the edges of the pit, and, meeting above the organ, form a short section of canal, the openings of which are inclined to the general surface, and give to the canal a tunnel-like appearance.* A narrow shallow channel, pigmented like the rest of the outer surface, has meantime formed between the organs along the bottom of the general depression. It is deepest near the newly formed section of canal; and into it the canal opens, the sides of the openings passing gradually into the walls of the channel. The limits of the canal are clearly defined by a sharp change in direction of the bottom of the channel, the canal leading inward at something of an angle, the walls of the canals and pits always being much lighter in color than the outer surface. *The openings of these short sections of canal may be called half-pores, because, with a few exceptions, all the primary pores in the developed system are formed by the fusion of two of them* [italics mine]. *After its formation the short canal increases in length by the continued coalescing of the edges of the channel immediately beyond it, and the two half-pores are pushed apart along the line of the canal toward other pores, which are in a similar way approaching them from adjoining sections.* This process in Amia is continued until the pores meet and unite, thus forming a continuous canal with a primary pore and tube between every two consecutive organs; but it may be arrested, in which case an interrupted canal will be formed. At each end of a continuous canal formed in this manner it is evident there must be a pore, which, if it cannot unite with a pore of some other line to form a double system, must always remain a half-pore or terminal opening.

"These two processes are continuous and essentially similar; for even in the adult, two pores if forced together from want of space, fuse."

The little that is known of the development of the canals and their organs in the bony fishes agrees essentially with this account of their development, but we have no such complete history of canal development among other ichthyopsoid types.

Let us now turn to the embryology of the vertebrate auditory organs and examine the facts which have been accumulating for many years, contributed from many different sources. Some of the conclusions now accepted will doubtless change in time,

but the majority of the facts of the development of this complexus have been so often studied and the results of the earlier observers so often confirmed that as regards the mode of development there can be little question. It will be noticed, I think, in the accounts which I shall give of the ontogeny of the ear in the various types, and which I shall endeavor to make as complete as possible, that there is a remarkable absence of any attempt to account for the phylogeny of the vertebrate ear with the facts derived either from ontogeny alone or from comparative anatomy and development combined.

The ontological history of the lateral line organs of Sharks and Skates is up to the present but partially recorded, and the subject is one demanding thorough investigation, both from its intrinsic interest and the very great importance of its relation to the morphology and physiology of sense organs in general. I have not the necessary material for a complete history, and shall attempt here only a brief sketch of some of the important stages of the development of the lateral line organs of the head, in so far as they have a direct bearing upon the question of ear production and an anatomical connection with the specialized canal complex known as the internal ear. The early stages of these organs have been studied by many investigators, notably Balfour, Beard, Mitrophanow, and Semper. The later stages have been almost completely neglected. As is well known, the auditory thickening, soon converted into a cup or pit (Pl. I, Fig. 6, Cuts 17, 18, 19), appears long before the other parts of the lateral line system are established, but as it sinks below the surface it retains its connection with the surface of the body by means of a canal, the endolymphatic duct of later stages. This canal opens out into a groove on the surface of the head which is lined by a peculiar and characteristic epithelium. Owing to the concomitant growth of the head and the closure of the auditory groove, the first of which is the main cause, while the latter is mainly a result of the transposition of the ear complex already well below the surface of the head and surrounded by a semi-fluid mesodermic tissue, the ear hole, or orificium ductus endolymphatici, travels forward, the epithelium of the groove increasing to an extent sufficient to maintain the anatomical connection of the sunken ear with the sensory epithelium on the surface of the body, which later events prove to have only

been partly used up in the formation of the ear. A glance at Figs. 15, 16, Pl. I, and Fig. 4, Pl. IX, will show how beautifully and completely this connection is kept through the vicissitudes of the ontogenetic changes.

When the lateral line organs have made their appearance, the auditory grooves communicate with their line at points equidistant from the median line on either side of the head. The preservation of the anatomical continuity of the internal ear with the surface organs of the lateral line system is sufficient evidence to establish the thesis on my title page were no other evidence forthcoming. This structural continuity is broken later on in most Elasmobranch species, though it persists in a few forms throughout adult life. In the young Torpedo (Pl. I, Fig. 16) the relation of the end of the auditory groove to the aural sense organ canal is still plainly visible. The groove ends between two sense organs and marks the place from which the original sense organ of the ear migrated.

Development of the Organs of the Lateral Line in Ichthyophis according to the Brothers Sarasin.

The first traces of the lateral line organs appear very early in development. They are first indicated by a thickening of the epidermis in more or less circular patches, which thickening is due to a lengthening of the epithelial cells of both layers, but most noticeably of the outer layer. The apex of the organ sinks inward, while at the same time the cells of the lower layer grow longer in a narrow circle which surrounds the central depression, thereby making its walls higher and the pit deeper. One or more of the cells of the outer layer which lie in the centre of the depression grow larger and rapidly assume the form of the adult sense cells. They soon occupy the entire thickness of the epithelial layer from the bottom of the pit to the basement membrane. The Sarasin brothers believed that all other sensory cells of an organ were produced by the division of a single cell, the "Sinnesurzelle."

The epidermal cells of the second layer, which lie immediately underneath the sense cells, are shoved to one side and begin to lengthen, sending a prolongation upwards around and among the sense cells; when fully developed, they form the long staves or supporting cells of the completed organ.

They recognize three forms of this kind of sense organ, which they designate as

1. Sinnesurzelle = Stiftchenzelle.
2. Becherorgan.
3. Geschmacksknospe.

In this account of the surface sense organs of Ichthyophis, the Sarasin brothers (1890, 248) describe a second kind of organ found by them, which they call an "Accessory ear" or "Flask-shaped" sense organ. The body of such a sense organ is more or less flask-shaped with a central lumen which has to a greater or less degree the shape of the organ. Within this cavity freely suspended, perhaps supported on the ends of the sensory hairs, is a club-shaped, highly refractive body, which is largest at its inner end and gradually tapers outward, ending just at the level of the surface of the skin, never projecting beyond it. This body the authors call the "keulenförmiger Körper," and suppose it to be composed of a homogeneous and coagulable secretion.

The walls of the organ are divisible into two very distinct parts, an upper and outer or communicating tubular portion, and an inner or basal sensory portion. The walls of the former are composed of ordinary epithelial cells, while the latter is composed of the thickened sensory epithelium — some of the cells of which are hair bearing. These sense cells are probably derived from a division and aggregation of primitively isolated nerve end cells (Sinnesurzellen), which by the development of surrounding and supporting cells produces the taste bud or associated sense organ.

The innermost layer of cells is composed of pear-shaped sense cells, each of which bears a distinct, stiff, refractive hair which runs to the surface of the club-shaped mass and inserts in it. Consequently the club rests upon the points of the hairs of the sensory cells. A boundary between hair and sense cells the Sarasin brothers were unable to find.

The ganglion below the sense organ develops only after the larva enters the water. The function of these organs is doubtless that of hearing. The little club which rests on the hairs they designate the auditory club. The organ itself is the accessory ear of the Ichthyophis larva.

In this organ we have represented all the essential parts of

the canal organ, leaving out of consideration the canal itself; but as I have already shown, the only unusual structure, or the auditory club, present in the organ is without doubt an artifact, produced by the transforming action of the reagents used in preserving the larvæ.

Leydig (1850, 179) was probably the first author to connect in thought the surface canals (knowing their structure) with those of the ear. In this paper he calls attention to the similarity of the so-called mucous canals with the ampullæ of the ear, but later he was inclined to consider the lateral line organs as tactile organs possessing a function unlike all others, and which he suggested might be a sixth special sense.

The idea advanced by F. E. Schulze (254) in 1861, that the lateral line organs were probably affected by the water waves of longer wave lengths, and also by the movements of masses of water, had the advantage of being specific; and to-day the mass of evidence sustains his view.

Dercum (1879, 71) considered the sense organs of the lateral line so similar to the maculæ of the ears, that he applied the term maculæ laterales to the former, and instituted a comparison of parts between ear and lateral canals more detailed than had previously been attempted.

Emery first described the cupula terminalis in the lateral canals of Fierasfer, and compared these structures with those of the ear.

Mayser's views I have already partly given. The posterior root of the VIII together with the recurrens superior form the nervus lateralis. The second branch of the V supplying the "Nervenhugel" is given off from the VIII. Mayser concludes that while it will be impossible to state definitely that these organs transmit sound waves, yet their function undoubtedly falls within the province of the auditory sense still so incompletely known.

Bodenstein[1] (1882) went further and compared the lateral canals with the membranous canals of the ear; the endolymph he found represented by the fluid in the lateral canal; the bony canal was present as the denser investment of the lateral canal; and he concludes that the lateral canal system is probably an *ontogenetically later appearing repetition of the auditory organ!*

[1] *Zeitschr. für wiss. Zool.* XXXVII, 1882.

Wright (293, 1884) has described the sense organs of the Catfish (Amiurus) with histological detail, and he concludes that they are organs for the perception of wave motion.

Fritsch (93c, 1889) found an astonishing agreement between the structure of the sense organs of the lateral line and those of the ear, and found the hairs of the former of considerable length, but failed to find a cupula, although he thought one probably existed.

The *Sarasin* brothers thought to have found three sorts of sense organs which form a graded series of auditory organs from the simplest condition up to the stage represented by the vertebrate ear, on the surface of the body, and in the head of the larval *Ichthyophis glutinosus*. They classified them as

1. Naked Nerve Hillocks.
2. Accessory Ears or Nebenohren.
3. The Ear.

They recall the fact that all the lower forms possessing the lateral line organs lack the cochlea; but as they lose the lateral line organs, the cochlea grows more and more in size, becoming ultimately the most important section of the ear.

The "Seitensinnorgane," as described by Krause (1885, 169), have much in common with taste buds, but must be separated from them for the present. They are dermal nerve end organs composed of elongated epithelial cells, and are found in *Amphioxus*, Teleosts, and aquatic Urodela and Anuran larvæ. Among these forms they occur abundantly. They are placed on the head, follow the course of the rami laterales n. vagus over the trunk, and probably on to the tail. These have received very numerous significations. Merkel (1880, 295) separates them from taste buds or terminal buds (Endknospen), which likewise occur on the bodies of fishes; they are, nevertheless, tactile organs. I cannot enter here upon the tracing of these organs among the phylogenetically older fish species.

The simplest of these organs are probably tactile organs, but fishes do not "feel" with their bodies, endeavoring merely to prevent any contact with bodies denser than water. F. E. Schulze designated them organs for the perception of wave motion (Wellensinnesorgane). But waves do not occur in the deep waters, and the resistance of the water is apprehended by

the muscle sense. Considering their extreme likeness to taste buds, it is most probable that they serve to give notice of chemical and physical changes in the surrounding water (Krause, 1875). Fishes are very sensitive to lack of oxygen in water, die readily from such cause, and seek to avoid such water, but they probably possess little sensibility to alkaline water.

From the foregoing statements it is evident that the similarity of many structural details between surface organs and subdermal ear organs has been recognized by many writers, and the functions of the two sets of organs been connected analogically, but no one has yet claimed, much less produced, the proof that these structures are genetically related in the very intimate manner I have shown them to be. The importance of these facts for the unravelling of the tangled skein of ear development can hardly be overestimated.

F. E. Schulze (1870) says, p. 63: "Aus dem ebenen oder leicht concaven Gipfelfelde einer solchen, wesentlich aus cylindrischen Epithelzellen bestehenden hügeligen Hauterhebung, in welche von unten her ein Nerv eintritt, sah ich eine Anzahl feiner starrer Haare rechtwinklig zur Oberfläche parallel ins Wasser hinausragen, sehr ähnlich den auf der Crista acustica der Ampullen gefundenen, nur bedeutend kürzer als jene. Diese starren Härchen liessen sich mit einer geringen conischen Verbreitung in gewisse helle den Hügel selbst durchsetzende, andererseits aber mit den aufsteigenden Nervenfasern in Verbindung stehende Züge verfolgen, so dass auf einen direkten Zusammenhang der Haare mit den Nervenfasern geschlossen werden durfte. Ferner beschrieb ich eine zarte helle Röhre, welche von dem oberen, die haartragende Fläche des Hügels umgrenzenden Randsaum entspringt, das Haarbündel umschliesst und dasselbe mehrmals an Länge überragend, an dem aüsseren Ende offen und quer abgestutzt, rechtwinklig zur Oberfläche des Thiers frei ins Wasser hinaussteht."

The sensory cells were about 0.01 mm. long, while the hairs they bore measured, in the "Kaulbarsch," from 0.012 to 0.014 mm. long. Schulze followed the nerves as fine non-medullated fibres up into the cells and considered the hair to be continuous with the nerve.

(P. 84.) "So wenig nun auch daran gedacht werden kann, die Seitenorgane als wahre Hörapparate anzusehen, nicht allein

deshalb weil Fische wie Amphibien schon ein entwickeltes, durchaus nach demselben Typus wie bei den Wirbelthieren gebautes Gehörorgan besitzen, sondern besonders deshalb, weil sich immerhin noch erhebliche Unterschiede in den Bauverhältnissen zwischen beiden Organsystemm finden — so werden wir doch von einer Vergleichung mit den Gehörsinneseinrichtungen unter Berücksichtigung der bestehenden Unterschiede ausgehen müssen. Der wesentlichste Unterschied besteht aber meiner Ansicht nach darin, dass die Nervenendhaare der Seitenorgane nicht wie die Hörhaare in eine allseitig eingeschlossene Flüssigkeit, wie es die Endolympha ist, sondern frei in das *äussere Wasser* hineinragen und, was mir besonders wichtig erscheint, *weit kürzer und etwas derber* sind als jene, welche bekanntlich in eine lange, äusserst feine Spitze auslaufen. Wie nun die Hörhaare durch gewisse Bewegungen des Mediums, in dem sie sich befinden, der Endolympha, nämlich durch die Schallwellen in Mitbewegung versetzt eine Nervenerregung veranlassen, welche zum Gehirn fortgeleitet dort zur Sinnesempfindung des Hörens führt — so werden auch die Sinneshaare der Seitenorgane sicherlich durch gewisse *Bewegungen* der Flüssigkeit, in welche sie hineinragen, nämlich *des äusseren Wassers, in Mitbewegung versetzt* die Erregung der zuführenden Nervenfasern und mittelst dieser eine Sinneswahrnehmung herbeirufen"; and he concluded that these sense organs perceived only the motion of masses of water and the heavier, longer, water waves, *i.e.* those which would not suffice to give rise to sensations of sound. This conclusion was reached on the basis of the shorter and stiffer hair, which he claims to have found regularly on the external organs. In the ampullæ of the ear the greater length and delicacy of the hairs would permit of a greater delicacy of perception.

Fritsch (1887, 93[b]), in describing the lateral line organs of Malopterurus, says of the sense organs which he discovered in the lateral canals (p. 48): "Ein höchst bemerkenswerther Punkt, der mir, wenn auch gelegentlich angedeutet, doch nicht genügend hervorgehoben scheint, *ist die erstaunliche Aehnlichkeit des histologischen Baues der Endhügel mit demjenigen der Maculæ acusticæ im Gehörorgan der Fische.*"

"Vergleicht man die ebenso gründlich ausgeführten, wie prächtig illustrirten Arbeiten von Hrn. Gustav Retzius über

den Gegenstand, so ist man fast in Verlegenheit, wesentliche Unterschiede namhaft zu machen, wenigstens gilt dies für den hier behandelten Fisch." On p. 49, our author continues: "Ein Moment, wodurch die Endhügel des Zitterwelses den Maculæ acusticæ noch besonders ähnlich werden, ist die starke Ausbildung der haarförmigen Verlängerung auf den Sinneszellen, welche hier eine beträchtliche Länge erreichen, während sie bei anderen Fischen gewöhnlich nur die Gestalt kürzerer Borsten zeigen sollen. Der auch sonst beschriebene breite, basale Ansatz des Haares auf der Zelle kommt hier gleichfalls zur Beobachtung."

"Zur Vervollständigung des Bildes würde es dienen wenn die Sinneshaare bedeckt gefunden wären mit einer sogenannten *Cupula;* eine solche ist aber mit Rücksicht auf die Conservirung *ohne Anwendung von Osmium nicht wohl zu erwarten* [italics mine]. Was die Auffassung dieser merkwürdigen, die Sinneshaare wie eine streifige Kappe bedeckenden Formation anlangt, so schliesse ich mich ganz an Hrn. Retzius an, welcher das Zustandekommen der auffallenden Bilder im Präparat durch die unter Osmiumeinwirkung erfolgende Gerinnung einer schon bei Lebzeiten zwischen den Haaren befindlichen, fein gestreiften Substanz erklärt. Danach ist also nur die Form unter welcher sie in den Präparaten erscheint, durch die Behandlung hervorgerufenes Kunstproduct, und es ist durchaus wahrscheinlich, dass durch ähnliche Methoden der Conservirung, wie sie zur Darstellung der Cupula in Anwendung kamen, auch an den Seitenorganen des Zitterwelses eine solche Umhüllung der Sinneshaare sichtbar zu machen wäre."

This investigator studied Savi's vesicles, and writes of them, p. 83:

"Nach Durchbohrung des Polsters [the basal plate of Savi's vesicle, which is homologous with the floor of the ampullar organ] pflegt der Nerv in drei Theile zu zerfallen, von denen der mittelste der stärkste ist, die beiden anderen aber ausnahmslos in der Längsrichtung der ganzen Bläschenschnur angeordnet gefunden werden," and each nerve bundle ends in a well-formed sense organ. Fritsch characterizes this condition further by saying that "jedes der drei Aestchen eine Art Sohle ausbildet"; and "Eine vollständig ausgestattete Blase hat also drei Sinnesinseln, an deren Grenzen mit den Nerven auch

die Sohle sofort verschwindet, das Epithel aber einen ganz abgeplatteten, Endothelartigen Charakter annimmt so dass es auf der fibrösen Bläschenwand im Durchschnitt nur als ein schmaler Saum erscheint.

"Die langen haarförmigen Anhänge der Sinneszellen sind sehr vergänglich und lassen sich nur am frischen Präparat . . . erkennen."

"Zu den mancherlei Analogien, die sich zwischen den in Rede stehenden Organen und Theilen des Gehörs finden, kommt als weiteres Moment hinzu, dass die Haaranhänge der Zellen sich bei beiden Anlagen leicht in der längsrichtung spalten, wie es besonders Hr. Retzius von den Haaren der Hörzellen genau beschreibt und abbildet."

"Dabei findet jedenfalls auch ein Durchtritt von Secret sowie von lymphoiden Zellen zwischen den Elementen des Sinnesepithels statt; dasselbe zeigt sich von jener eigenthümlichen Kappe bedeckt, welche von den Autoren die Bezeichnung 'Cupula terminalis' erhielt. Sie wurde in den SAVI'schen Bläschen, wie es scheint, völlig übersehen, obwohl sie gerade hier besonders kräftig entwickelt ist und schöne Gelegenheit bietet, die Art ihres Aufbaues zu studiren."

"Die Ergebnisse der Untersuchung sprechen durchaus dafür, dass die *Cupula* ein Secret der Stützzellen unter Betheiligung durchtretender lymphoider Elemente, die sich zuruckbilden oder auflösen, darstellt. Eine ähnliche Ansicht hat auch bereits, wie mir später bekannt wurde, Hr. Solger ausgesprochen und in neuster Zeit sind die Hrrn. Sarasin in ihren schönen Untersuchungen über ceylonische Blindwühlen in Betreff der *Cupula* auf den Seitenorganen zu derselben Ueberzeugung gelangt, welche auch von Hrn. Fr. Eilhard Schulze vertreten wird."

"Es entspricht dieser Vorstellung, dass die eigenthümliche, im frischen Zustande glasshelle Kappe in verschiedener Höhe über dem Epithel erheblich abweichende Bildung erkennen lässt. In dem Bereich der Sinneshaare, wo das Secret zugleich das frischeste sein muss, trägt es einen mehr dünnflüssigen Charakter, so dass die einzelnen Haare in cylindrischen Hohlräumen der Cupula frei spielen können, und die ganze Kappe von unten betrachtet ein wabiges Ansehen darbietet. Die über den Stützzellen aufsteigenden Secretmassen gewinnen also erst in einigem Abstand eine zähere Beschaffenheit und geben

der Masse von der Seite betrachtet das bekannte streifige Aussehn."

"Selbstverstandlich wird die *Cupula* durch die vorgenommene Behandlung der Objecte beeinflusst, aber ebenso sicher ist es auch, dass man aus dem bestimmten, der Umgebung angepassten Verhalten dieses so verbreiteten Aufsatzstückes auf den Sinneshügeln schliessen muss, die Natur liefere dafür schon eine Grundlage, welche gewiss nicht ohne Bedeutung für die Function ist." Our author was not able to find the cupula in the lateral canals, if we except a single instance when he observed "nur ein unregelmässiges, faseriges Gerinnsel," and he accounts for this condition by assuming that the cupula secretion is too thin to stick to the sense organ. It is important to note, however, that he did find the hairs much longer in the sense organs of the lateral canal than in the other structures, where he found the cupulæ well developed.

If, as he assumes, in harmony with the rest of the cupula defenders, this is a secretion of compound nature poured out between the hairs and surrounding them with a jelly-like sheath, it is fair to ask what becomes of the older portions of the cupula as additions are made to its base. For it is evident that this secretion must go on continuously if secretory cells, as holders of this view claim, are present among the sensory cell group. It would be necessary to assume a constant resorption of such mucoid secretion. Now, while there is no question that some mucus is present in all cases (all in which exact analyses have yet been made), there is no evidence to show that in a state of nature it exists as a dome-shaped mass covering the sense organ. On the other hand, it is clearly proven that the most typical cupulæ yet studied are products of the action of reagents, and that so far as fibrous structures in the channels occupied by sense organs (whether ear organs or those of the lateral line system) are concerned, they have in every thoroughly studied case shown themselves to be hairs more or less unchanged. Fritsch concludes by explaining that the free access of water to the lateral canals would wash out the mucoid cupula which, in the case of the vesicles of Savi and of the ear, would be retained.

The special form of sense organs, known under the name of Savi's vesicles, have a peculiar interest for us at this time,

since they are without doubt descendants of the canal organs. Fritsch has traced their development sufficiently to give us assurance that they are transformed from the canal type during ontogeny.

Fritsch describes the processes of growth which determine whether the canal line which, in the majority of Batoid forms, occupies the place, and has the other anatomical relations, of the line of Savi's vesicles in the Torpedinidæ is to grow into Savi's vesicles or to remain a canal line. He says, "Verschmelzen die dünnwandigen, aber festen bindegewebigen Häute, welche den Lymphraum begrenzen, da miteinander, wo sie zwischen den Sinneshügeln an einander stossen, in vorwiegend sagittaler Richtung, so werden Canäle daraus, Verschmelzen sie allzeitig an den Grenzen der Ausbuchtungen für die Sinneshügel, so werden aus diesen SAVI'sche Blasen."

As to the identity of position in the two groups of Batoids, he observes, "Wie die Reihen der SAVI'schen Blasen von der Ventralseite vorn an der Schnauzenkante zur Dorsalseite treten, so treten an gleicher Stelle die ventralen Kopfcanäle der gemeinen Rochen in die Rückencanäle über." Our author mentions transitional stages between the open canal and the closed vesicular organs, and after stating that in histological characters the two sets of organs likewise agree, concludes that "Aus allen diesen Vergleichungen ergiebt sich, dass die SAVI'schen Bläschen abgerundete und gänzlich abgeschlossene Stücke haütiger Kopfcanäle anderer Rochen darstellen," and that we need no longer be surprised that the Torpedoes possess a system of organs which is lacking in all other Batoids, but which is represented in these forms by the more primitive canal type.

The special interest which Savi's vesicles have for us at this time is due to the fact that they constitute a second closed system of organs derived from the wide-spread, open canal type, and which in this respect have advanced along the same line of differentiation as the auditory organs, and must be subject to the same conditions as the ear hairs in the reception of sound waves, he adds (p. 133): "Die unter verschiedenen Namen, wie Seitenkanalsystem, SAVI'sche Bläschen, und LORENZINI'sche Ampullen, bezeichneten Canäle unter der Haut der Torpedineen stellen verschiedene Glieder eines in der Uranlage einheitlichen

Systems mit specieller Anpassung an die Function im Sinne der Arbeitstheilung dar. Von diesen Gliedern sind das Seitencanalsystem und die Savi'sche Bläschen mit Sinnesepithelien ausgestattet, die Lorenzini'schen Ampullen nicht: vielmehr dienen letztere secretorischen Functionen." And he concludes, on p. 92: "Ich schliesse mich daher in vollster Ueberzeugung denjenigen Forschern an, welche die Meinung vertreten, dass die Uebereinstimmung des ganzen Aufbaus der Seitenorgane mit Gehörorganen auch zur Annahme einer wenigstens ähnlichen Function berechtigt, d. h. dass die Nervenhügel bestimmt sind durch das Medium fortgeleitete Schwingungen wahrzunehmen, wie unter Anderen auch von Fr. Eilhard Schulze angenommen worden ist. Die Entgegnung, dass die Fische ja so schon Gehörorgane besitzen und daher anderer, verwandter Sinnesorgane nicht bedürften, vermöge ihrer günstigen Lage Schwingungen, die noch nicht als Ton wahrgenommen werden, oder selbst einfache Erschütterungen des Mediums mit grosser Schärfe erfasst werden könnten, während die eigentlichen Ohren noch nicht oder wenigstens nicht in gleicher Weise darauf reagirten."

The physiological process takes place in the epithelium of the sensory organs of the lateral line organs of fishes, according to Dercum (1879, 71), *loc. cit.* pp. 152–154, in this manner: "The true detailed action of these organs is probably as follows: Let us suppose any disturbing cause to set up in the water a wave of long period. It impinges, first, on the membranous interspaces or drum heads before spoken of, and with the greatest intensity, of course, on those which are most nearly placed at right angles to its direction. The wave is thus communicated to the liquid in the canals, which transmits it to the adjacent masses of jelly-like mucus covering the disks. The quivering of these little masses probably excites and intensifies vibrations of the hairs of the perceptive cells. The fish probably judges of the direction of the disturbing cause by the portion of the apparatus most strongly excited. The membranous spaces or drum heads, when the apparatus is well developed, are so arranged as to favor the perception of vibrations from almost all directions." In view of the structural resemblance of the sensory disks to the maculæ acusticæ, he calls them maculæ laterales.[1]

[1] See Recapitulation C.

D. EMBRYOLOGICAL.

An account of the successive stages in the early development of the internal ear in the following vertebrate types: —

1. Pisces. Petromyzon, Galeus, Acipenser, Salmo.
2. Amphibia. Rana.
3. Reptilia. Lacerta, Tropidonotus.
4. Aves. Gallus.
5. Mammalia. Lepus, Ovis, Bos, Sus, Felis, Homo.

The Ontogeny of the Ear in the Several Classes of Vertebrates.

Valentine (1839, 279) first described the formation of the semicircular canals of the vertebrate ear. He states that they form by the growth of blind pockets of the utriculus, in a semicircular manner, out from the parent cavity, through the tissue of the head, until they come again in contact with the utricular wall, when they break through the walls at the point of contact, and by a fusion of the edges of the parts thus brought together establish communication by the curved channels between the two ends of the utriculus. This outgrowth of the tubular processes was followed by a wave of reduction of the bore of the canals, which stopped short of the end of the canals and thus left enlargements, the ampullæ, which, of course, represented the original size of the canals. According to Valentine, the posterior canal was first to form, the anterior following it. Our author did not observe the formation of the external canal.

Rathke (1839, 223), from his studies on the Adder (*Tropidonotus natrix*), could not trace the development of the semicircular canals as Valentine had described it; but found that each canal was formed independently by the closing over of the edges of a groove formed in the wall of the utriculus. The edges of the grooves or folds united first near the middle of the length of the groove and grew each way toward the ends of the utriculus. It is at the point of contact that the separation of the canal from the utriculus first takes place by the resorption of the tissue composing the fused folds. The canals grow rapidly in extent after separation begins. Three years later his results were confirmed by Gunther (1842, 107) for mammals, and by Bischoff (1842) for birds.

Vogt (1842[1]) agrees with neither Valentine nor Rathke, but was not certain that he had rightly interpreted the processes of canal production. He thought they were produced by the growth of the cartilaginous capsule forcing in the walls of the auditory vesicle until the folds thus formed met and produced the canals. He did not observe the development of the sensory epithelial structures.

Reissner (1851, 228) and Rosenberg (1868, 242) agreed in all essential particulars with Rathke. Their observations were made on mammals.

Boettcher (1869, 31) was the first accurately to describe the origin of the two vertical canals in mammals from a common furrow.

Goette (1875[2]) described the development of the Amphibian ear in his studies on Bombinater. And his account of the development of the semicircular canals shows that they developed in the same manner as in mammals according to Boettcher's account.

Von Noorden (1883, 205) devotes much care to working out the transformations of the auditory vesicle in bony fishes, and by means of direct observations on the transparent living embryo, by means of sections, and also by means of models reconstructed from serial sections, he was able to give us the most accurate as well as the most detailed account of the morphological changes which the ear undergoes in development, that we have of the Teleosts. His observations were made upon eight species, including the European trout, salmon, and herring.

Rüdinger (1888, 244) returned to the old theory of Valentine. This he somewhat modified. He says (*loc. cit.*):

"1. Die Bogengänge entstehen durch epitheliale Knospung oder Sprossung aus der Ohrblase.

"2. Für jeden einzelnen Bogengang treten zwei Sprossen auf.

"3. Die Vereinigung der beiden Sprossen kommt zu Stande durch die Grössenunterschiede der Zellenmaterials an der convexen und concaven Seite eines Bogengangs." Rüdinger claims to have found the canals in their first stages of growth as blind pockets leading out of the utriculus.

His (1889, 137) describes the formation of the canals in the

[1] *Embryologie des Salmones.* Neuchatel.

[2] *Entwicklungsgeschichte der Unke.* Leipzig.

human embryo in a manner entirely in harmony with Rathke's account.

Villy (1890, 281) described the development of the frog ear, and devoted especial attention to the early stages of the formation of the canals and the division of the sense organs.

Krause (1890, 169[b]) criticises Rüdinger's observations, and proves that Rüdinger had mistaken the ductus endolymphaticus in his sections for the external canal. Krause has thoroughly worked out the history of the ear canals, and he is the first to recognize that, in the Mammalia, the ampullæ are marked out before the canals are formed. They are formed, as I can state, as sense-organ pockets. He, however, does not recognize the significance of his discovery in its bearing upon the phylogeny of the ear sense organs.

During this time the study of the adult anatomy of the internal ear was making great progress. Our knowledge in this department was very incomplete until about the year 1865, which, though only an approximate date, may serve to mark the beginning of the more recent movement in the study of the vertebrate ear which has culminated in that magnificent outcome of the united labors of many of the keenest scientific minds of the last quarter of the century, brought together, critically revised and combined with a very large number of original observations, remarkable for their accuracy and completeness of detail, — entitled *Das Gehörorgan der Wirbelthiere* by Gustav Retzius.

Development of the Ear in Cyclostomes.

The developing auditory vesicle of *Petromyzon fluviatilis* presents many interesting characters which have been only recently made known to us by Kupffer in his beautiful study of this form. The capsule invaginates from the ectoderm *as one of a series of invaginations* occurring along the side of the head in connection with the formation of the cranial ganglia of the lateral group. The Trigeminus invaginations are most conspicuous, and give one the impression that we have to deal with the formation of similar structures. Kupffer calls attention to this resemblance, but does not conclude that these are strictly homologous. He says (*loc. cit.* p. 522): "Das Verhalten der Epidermis zu dem massiven Ganglion [*i.e.* the ganglion

of the Trigeminus nerve] ist in *Zeitpunkte der Abschnürung beider Gebilde ganz übereinstimmend.*" These invaginations are connected by a ridge of thickened epithelial cells. I regard this as proof of the strict homology of the ear sense organs with the sense organs belonging to the Trigeminus and Vagus groups of nerves. Soon after the invagination, the internal ear of Petromyzon presents a round appearance, and by the sixth day has assumed a somewhat hemispherical shape. With a dorso-median portion of the auditory flask one of the branches of the dorsal root of the auditory nerve has come in contact. Later on there appears a fissure in the part of the wall of the auditory vesicle, and the auditory nerve makes its way into its future internal territory of distribution.

In Shipley's (1887, 261) paper on the development of Petromyzon, he describes the growth of two thickenings of the epithelial wall which arise from the anterior and posterior inner angles (if one may speak of these portions of the curved walls as angles) of the auditory vesicle. The formation of the canals is a later phenomenon, and they are first marked off, as Scott has found, by the outgrowth of two folds from the outer and inner walls of the vesicle which grow toward each other. The inner process is situated higher up and just external to the *recessus labyrinthi.* In the next stage the two processes are in contact, and then coalesce, dividing the vesicle by means of an oblique partition into two chambers. In the middle of the dorsal wall the partition is incomplete, and here the two chambers communicate.

Kupffer found in the larvæ of Petromyzon Planeri (Ammocœtes) that in its earliest stage the auditory involution is represented by "eine etwas unregelmässige Einsenkung der Epidermis, deren Zellen hier etwas verlängert sind und durch den Vorgang, der sich vollzieht, eine Aenderung ihrer Gestalt erfahren. Dadurch wird der eingesenkte Abschnitt etwas dicker, als die nächste Umgebung.

"Ventralwärts hiervon erscheint eine neue Epidermisleiste, die sich durch Verlängerung der Zellen und mitotische Figuren bemerklich macht.

"Die Nervenanlage besteht aus einer Reihe dicht an einander gelagerten Zellen, die aus der Decke des Hinterhirns hervorgeht und ein freies Ende hat, denn die letzte konisch gestaltete

Zelle liegt frei zwischen der Seitenwand des Hirns und dem Boden der Labyrinthgrube. Am Ursprunge der Reihe sieht man die erste Zelle eingeklemmt zwischen den Cylinderzellen der Hirndeckes. Hier kann gar kein Zweifel über den Ursprung dieser Bildung bestehen, dieselbe wächst aus der dorsalen Region des Hirns hervor und stellt die Anlage des Acusticofacialis dar."

Later on the pit assumes hemispherical shape and "die dorsale Wurzel hat sich gespalten, der eine Zweig verbindet sich intim mit der dorsalen Wand der Hörgrube, der andere Zweig umgreift die Grube an ihrer medialen Seite, verbindet sich einerseits mit den dorsalen Kantenzellen des Mesoderm, und zieht dann weiter zu einer Zellengruppe (Ganglion), die ventral von der Hörgrube gelegen ist, und sich an die Epidermisleiste anlehnt, deren Entstehung sich bereits fruher ankündigte."

Kupffer found the relations of the acustico-facial complex more complicated than those of the V. The auditory cup in involution presses against the brain wall, and the auditory nerve divides into two branches, an anterior and a posterior one. Kupffer does not recognize the formation of a nerve to the endolymphatic duct or describe it as the facial accessory nerve.

Kupffer found a great similarity between the ganglia of the V and X and auditory involution of the VII.

When the auditory involution assumes an oval form its long axis is nearly vertical, and the ventral wall is composed of much larger cells than the rest of it, and it is open at the top, and into this wedge-shaped cleft the fibres of the auditory nerve make their way to end in small oval bodies in contact with the inner wall of the vesicle. This nerve is the equivalent of the r. duct. endolymphatici, for the acustico-facial ganglion supplies the rest. Our author says further (*loc. cit.* p. 523): "Jedenfalls ergeben diese Thatsachen, dass die Verbindung der Nervenfibrillen mit der Gehörblase sich nicht in der Weise vollzieht, dass das Fibrillenbündel, welches die Anlage des Acusticus darstellt, sich mit den äusseren Basen der die Wand der Gehörblase bildenden Epithelzellen in Verbindung setzt, sondern diese Zellen weichen an der Verbindungsstelle aus einander und schaffen so einen Kanal für ein tieferes eindringen der Elemente der Wurzel bis zur Höhle selbst."

Kupffer was certain that not all of the fibres of the dorsal

root went to the gap in the auditory vesicle, but that some of them went on by to connect with the facial ganglion, from which other nerves were given off. This facial ganglion, owing to its intimate relation to the wall of the ear vesicle and the constitution of the wall in this part, "gestatten den Schluss, das mindestens dieser Theil des Facialisganglions in derselben Weise aus der epithelialen Wand der Hörblase entsteht, wie andere Ganglien aus der Epidermis."

The posterior wall of the auditory sac lies in a vertical plane with the second gill pocket and above a ridge of epithelium which separates the two. "In dieser Region tritt ganz symmetrisch eine stark ausgeprägte Epithelleiste hervor, die medialwärts einspringt, auf ihrer oberen Fläche die Gehörblase trägt und mit der unteren Fläche die dorsale Wand der Kiementasche berührt. Hart vor der Tasche entsendet die Leiste eine einfache Zellenreihe zwischen Epidermis und Mesoderm ventralwärts. . . . Diese Verhältnisse sind nicht anders zu denten, als dass es sich hierbei um die Anlage eines Nerven der Vagusgruppe handelt. Ob diese Anlage jetzt bereits Verbindung mit dem Fascials oder dem Vagusganglion hat und wie diese Verbindung sich vollzieht, kann ich nicht mit Sicherheit entscheiden. Es scheint aber als wenn dass vordere Ende der Leiste von Zellen tangirt würde, die zu dem sichelförmigen Belag der Unteren Wand der Gehörblase gehören und die ich zum Facialisganglion rechne."

Kupffer recognizes differences between the ganglionic Anlage of the V and that of the VII, VIII, but concludes that they are nevertheless essentially the same.

The auditory sac remains single layered after complete separation from epidermis and the wedge-shaped split in its top closes, and develops in its place the endolymphatic duct (*reces. labyrinthi*), and in its neighborhood the nerve fibres end in the cells of the wall.

"Als Acusticus kann nach dem Mitgetheilten in vorliegender Entwicklungsperiode nur das Bündel von Fibrillen aufgefasst werden, welches die dorsale Region des Hirns mit der eben bezeichneten Stelle der Gehörblase verbindet und dabei muss noch besonders hervorgehoben werden, dass eine als Acusticusganglion aufzufassende Zellengruppe *zur Zeit nicht existirt*"; and, so far as it is known, never does develop in the course of

this bundle of fibres, which supplies only the dorsal part of the sac and the sense organ developed there, *i.e.* the two sense organs which have been described in a previous chapter as occupying places in one of the endolymphatic ducts and in the commissure of the semicircular canals.

"Unter Berücksichtigung dieser Umstände glaube ich annehmen zu dürfen, dass auch dem Facialisganglion ein spinaler und ein lateraler Antheil zukommen.

"Aber die Bildung des letzteren lässt sich von der Gehörblase nicht trennen, beide entstehen durch einen einheitlich zusammenhängenden Process, der in seiner Gesammtheit der Bildung der übrigen lateralen Ganglien zu vergleichen ist. Ich glaube, es lässt sich die Auffassung nicht abweisen, dass das Gehörbläschen in die Kategorie dieser Ganglien gehört. Dann würde dem Acusticus die Bedeutung einer spinalen Ganglienwurzel zukommen." From what has been said above it follows that the lower nervous structure connected with the auditory sac furnishes the material for the auditory nerve so-called — that is, all except the accessorius ; and this view I am inclined to believe is the true one.

From our present knowledge of the development of the ear of Petromyzon as a typical representative of the Cyclostomous vertebrates, we may conclude that the sensory Anlage which lies in the auditory vesicle remains a unit until after the ear is well inclosed. It then buds off from both anterior and posterior ends a sense organ, which at once proceeds in the work of producing two ampulliferous canals. We know from the adult anatomy that the canals are completely distinct in both Petromyzon and Myxine.

The remaining portion of the sense organ Anlage is incompletely separated into two parts, but it is uncertain whether this separation had taken place before the canal organs of the anterior and posterior ampullæ were budded off. These two sense organs which remain in the utriculo-sacculus are the maculæ acusticæ utriculi et sacculi, respectively. The division of the parent sense organ leads to a partial division of the common chamber or canal, which is effected by the ingrowth of a median raphe dividing the auditory vesicle into utriculus and sacculus. There are some considerations which I have presented in connection with the discussion of the nerve supply

that point strongly to the conclusion that the sense organ *at the time of invagination was a double one derived from two sources.*

Later on, without, however, dividing completely, these two portions of the sensory apparatus give off each a bud which remains in structural continuity with the parent organ, but which comes to lie in a pocket formed by the pushing out of the anterior median and posterior median portions, respectively, of the utriculo-saccular cavity. These two buds are the sense organs of the recessus utriculi and lagenar pocket, and in this condition the Petromyzon ear remains throughout life, so far as these sense organs are concerned. The nerve supply to these sense organs is derived from the two branches, the ramus anterior or utriculi and the ramus posterior or sacculi. These nerves seek two widely separated brain centres, the ramus utriculi running forwards and the ramus sacculi backwards, for their central connections.

The commissural chamber is of course only a portion of the semicircular canals. Seen from above, the canals run obliquely from the middle of the inner edge of the vesicle to its outer corners, with but very slight curvature. In what manner and at what time the sense organ makes its appearance here is totally unknown, and there is urgent need of information on the ontogeny of this organ and its nerve.

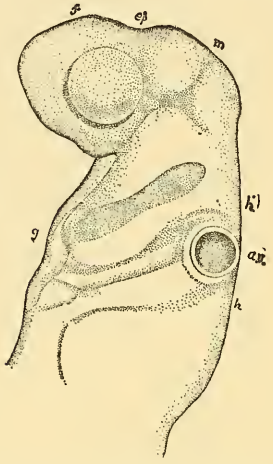
The Development of the Ear in Elasmobranchs.

Balfour (1876, 15) was the first author who began investigations on the ear of the Elasmobranch type, but his observations are very few in number and do not extend over any but the earliest stages of ontogeny. He closes his remarks on the embryology of the ear by observing (*loc. cit.* p. 188) that "with reference to the development of the organ of hearing, I have very little to say. Opposite the interval between the seventh and glossopharyngeal nerves, the external epiblast becomes thickened and eventually involuted as a vesicle which remains, however, in communication with the exterior by a narrow duct. Towards the close of stage K, the auditory sac presents three protuberances, one pointing forwards, a second backwards, and a third outwards. These are respectively the rudiments of the anterior

and posterior vertical and external horizontal semicircular canals. These rudiments are readily visible from the exterior."

His two figures are taken from embryos rendered transparent and sketched through the tissues from the side.

Mitrophanow (1890, 196), who has worked upon the lateral line system of Elasmobranch fishes, has recently announced that the auditory saucers and the sense organs of the lateral line system in the auditory region of the head have a common origin from a thickened band of epithelium, which begins in the spinal suture and takes in on both sides of the body the regions supplied by the VII + VIII and the IX + X nerves from where it descends to the gill region. First of all, the ear saucer separates from the sensory band which is thus cut in two parts, an anterior belonging to the VII, and a posterior lying in the territory of the IX. This separation is indicative of an earlier condition of independence, which has been obliterated by the shortening and modifying in other ways of the ontogenetic processes. This investigator observed epithelial ridges similar to those described by Kupffer in Petromyzon in the territory of the V, but he concluded that they were not related to the canal organs of the adult.



Cut 17. — The head of an embryo Shark (*Acanthias vulgaris*), from nature, magnified 20 times. The figure shows the saucer-shaped depression containing the insinking sense organ which is to be converted into the auditory sense organs of the Shark.

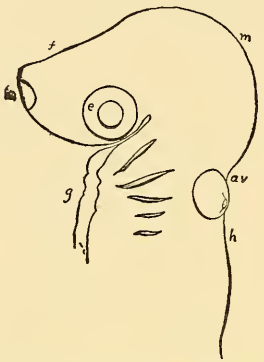
a.v Auditory saucer (vesicle).
ep Epiphysis.
f Fore-brain.
g Gill region.
h, *h'* Upper and lower hind-brain region.
m Mid-brain.

The early history of the development of the Elasmobranch auditory capsule does not differ materially from that of other forms except in the rate of growth. In this respect it is a much more favorable object for the study of the development of the internal ear than any other vertebrate with which I am acquainted. Cut 17 shows the auditory area of the skin after it has assumed the saucer shape, this condition of the organ following on the preliminary thickening of the

ectoderm and its sinking to the bottom of the saucer-like depression. The whole process of the formation of this cup is an exact repetition of the formation of a canal organ, and its canal as seen in Amia, or of the formation of an ampulla and its canal in the Salmon. As the saucer sinks below the surface, the opening on the surface grows smaller, the bottom of the saucer increases in size, and the resulting structure is an auditory vesicle distinctly flask-shaped. The neck of the flask grows longer, and finally appears bent backwards and inwards by the increase in size and length of the head region which carries the auditory capsule forward and outwards. During this lengthening of the neck of the flask, which is the endolymphatic duct of the adult ear, the body of the flask is much changed in shape. First of all it becomes compressed laterally, then it is drawn out in an antero-posterior direction, and concomitant with this elongation the anterior part points outward and the posterior part inward towards the median line. There may now be seen several changes in the shape of the vesicle, which, while not conspicuous, are very important, since they usher in a succession of transformations which ultimately produce the three semicircular canals and the rudiments of the cochlea. These changes are visible on the outer and upper faces of the vesicle as slight ridge-like elevations of the surface, and on the posterior ventral end of the vesicle as a knob-like prominence. Of the former there are two, of the latter a single one. The former structures seen from the inner face of the vesicle are merely depressed grooves in the wall of the vesicle, and the latter a sunken but broadly open pit. These grooves and pit grow deeper, the lips of the grooves come closer together, and finally in contact along the middle part of their course the edges of the pit are drawn closer together, narrowing its mouth. The lips of the grooves finally come in contact, fuse, and the grooves are converted into canals, opening into the auditory vesicle at each end. The auditory vesicle has become indistinctly divided into two parts by the formation of a constriction which arises somewhat obliquely off from both of the vesicles, and marks an anterior and a posterior chamber of the vesicle. From the lower part or sacculus the outgrowing pit or rudimentary cochlea has now become a deep pocket or blind canal, one side of which grows faster than the other, causing it to curve on its own axis. The canals which

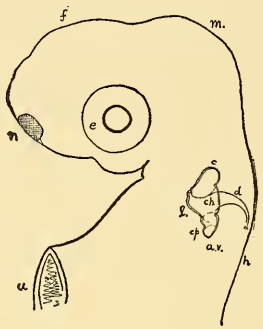
empty into the upper part of the vesicle or the utriculus are more distinctly marked off from the vesicle, and each presents at both its ends an enlargement, one of which contains a nerve end organ or a portion of the auditory sense apparatus. This is the so-called ampulla.

The other enlargement is non-nervous, and is the pseudo-ampulla, or, as I shall designate it, the *Ama*. With the formation of the three canals, their ampullæ and amæ, the cochlear canal and the more sharply defined separation of the utriculus



Cut 18. — The head of the embryo Smooth Dogfish (*Galeus canis*), seen from the left side. Figure drawn from nature, magnified about 20 times. The flask-shaped auditory vesicle is shown prominently placed above the gill region. Letters as in the preceding figure.

a.v Auditory flask.
e Eye.
f Fore-brain.
g Gill region.
h Hind-brain.
m Mid-brain.
n Nose.



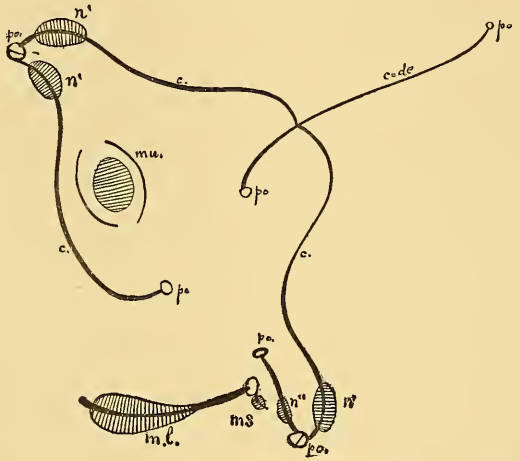
Cut 19. — The head of an older Shark of the same species, viewed from the left side. The figure, which was drawn from the living fish, shows the internal ear well advanced in its development. The rudiments of the semicircular canals and lagena are seen pushing out from the auditory sac (respectively the utriculo-sacculus, which has sunk far below the surface, with which it is, however, still connected by its sickle-shaped ductus endolymphaticus).

a.v Auditory vesicle.
c Anterior canal.
d Ductus endolymphaticus.
e Eye.
f Fore-brain.
ch External canal.
cp Posterior canal.
l Lagena.
m Mid-brain.
h Hind-brain.
n Nose.
u Umbilical cord.

from the sacculus, the Shark ear assumes the conditions and proportions which characterize it in the adult. The ductus endolymphaticus retains its connection with the exterior throughout life, and places the internal ear in communication with the

sea-water. In many forms of Elasmobranchs the ear contains scarcely any crystals, and not unfrequently sand grains are found within the ear. The sea-water undoubtedly plays a considerable part in removing the otoliths that are found in all species, by dissolving them.

The mechanical forces active in the modelling of the ear are for the most part the inherited tendencies of cell growth acquired as legacy from the canal organs of the surface of the body. The other forces are the pressures due to enlargement of ear and the concomitant reduction of space in which it has come to lie, the growth of the nerves into the ear, and the



Cut 20. — Diagram to illustrate the relations of sense organs of the ear when the ear vesicle is spread upon the surface of the head.

establishment of the vascular supply. The cochlear tube begins as a straight evagination, and curves soon after it comes in contact with the body wall. Inherited tendencies suffice to bring about the division of the primitive sensory area, the formation of the ampullæ, and the canals, except so far as the canals have a more or less curved outline. The canals are curved for the reason that they are formed as flattened pockets given off from a curved surface, and by the fusion of the edges of the fold along the whole mouth of the pocket, except at the two ends, where the tube thus formed opens into the utricular cavity at both ends. More clearly to understand that this is so, suppose the auditory vesicle with canals well formed be again drawn to

the surface of the head and caused to spread itself out flat. The inner face of its wall would thus form the surface of the head over the area covered. The canals would then appear as surface canals arranged somewhat as is shown in Cut 20. Here we find the canals inclined at varying angles to the long axis of the body. They form a group such as one may find on the head of any fish having the canal organs well developed; *i.e.* there is no essential difference between the relations of the parts as here projected and the canal organs on the surface of the body.

The Development of the Ear in Ganoids and Teleosts.

Salensky describes the development of the Sturgeon ear as follows (*loc. cit.* p. 307): —

"L'organe de l'ouïe, qui apparaît assez tôt, est représenté par les otocystes, situés de chaque côté de la moelle allongée, et resultant d'une invagination de la couche inférieure de l'exoderme. Il est probable que cette couche s'épaissit prealablement, car, après la formation des fossettes auditives, nous la trouvons plus épaisse autour de l'orifice de ces dernières. Déjà avant sa transformation en otocyste, la fossette auditive est pyriforme. Ses parois formées de cellules cylindriques sont épaisses dans le fond de la dépression, et sa cavité a la forme d'une fente triangulaire." "Vers la fin du développement, l'organe de l'ouïe a la forme d'une vésicule ovalaire, à parois assez minces formées de cellule cylindriques. Sous cet aspect, il représente l'ébauche du labyrinthe, aux dépens du quel se développeront dans la suite, les recessus labyrinthi, les canaux semi-circulaires et le canal cochléaire, toutes parties qui n'atteignent leur développement complet que pendent la periode post-embryonaire."

The auditory vesicle of the bony fish arises below the surface of the skin and does not present, as in the Shark, a genuine involution. There is, however, at a stage antecedent to the formation of the solid auditory sac, a thickening of the superficial epithelium behind the eye over the region occupied a little later by the auditory vesicle. It has not been ascertained whether this epithelial thickening is a superficial sense organ or not, and we know nothing of its fate or relation to the auditory organ within the head. The outer opening of the vesicle, *i.e.* the distal portion of the endolymphatic duct, places the cav-

ity of the vesicle in communication with the lymph space formed below the outer ectodermic layer. The vesicle is developed entirely from the nervous layer of the ectoderm, and agrees in this with the condition found in the Frog. The vesicle appears as a solid bulb of cells which pushes its way backward and inward towards the brain. Very early a cavity appears in the centre of the bulb and quickly extends up into the neck of the now flask-shaped structure. This prolongation of the vesicular cavity is the first stage in the development of the ductus endolymphaticus.

When the vesicular cavity has assumed a round oval shape, the cells forming its boundary walls, which, so long as the cavity bore the character of a split in the midst of the cell mass, were irregularly placed, arrange themselves regularly as a lining layer of epithelium, and thus pave the cavity smoothly.

Soon, however, the vesicle is compressed from side to side, and in connection with this folding process the epithelium thickens over three spots in the bottom of three depressed circumscribed areas, and long before there are canals formed these epithelial knobs have become provided with sensory hairs and constitute the three cristæ of the ampullary enlargements of the semicircular canals. Von Noorden describes this process as it occurs in the embryos of the Salmon and Herring. He says (*loc. cit.* p. 239): "Bald nach dem die Otolithen angelegt sind, beginnt auch an anderen Stellen das Epithel besondere Merkmale anzunehmen. An bestimmten Stellen bildet es sich wesentlich dicker als an der übrigen Blasenwand. Durch diese Dickenzunahme, welche durch ein Wachsthum der einzelnen Zellen in die Länge erzeugt wird, entstehen Wülste, welche in die Blase hineinragen und von vorn herein eine ovale Form haben. Die eine dieser Stellen liegt an dem Uebergang der äusseren Blasenwand in die vordere, die zweite an dem Uebergang der äusseren Wand in die hintere und die dritte an dem Uebergang der äusseren in die untere und zwar ist die Längsrichtung des Ovals bei den beiden ersten in einer Frontalebene, die Längsrichtung des Ovals bei der letzteren in eine Transversalebene des Fisches gelegen. Diese drei ovalen Epithelwülste bedeuten das erste Auftreten der Cristæ acusticæ. *Die Cristæ, später gelegen in den Ampullen der Bogengänge, treten also bei den Knochenfischen stets auf, ehe von den Bogengängen eine Spur vorhanden ist.*"

The transformation of the flattened, egg-shaped vesicle into the adult utriculus, sacculus, canals, etc., proceeds relatively slowly, and during this time the sensory tracts of the utriculus sacculus and lagena make their appearance as thickened areas of the walls of their respective chambers. In the Herring *the ampullary cristæ acquire their sense hairs and are in every way as perfect as in the adult before the walls of the ampullæ close over them;* while in the Salmon the canals are fully formed before the sensory hairs appear. The auditory hairs make their appearance on the inner ends of the now much elongated epithelial cells as minute conical protuberances, and by rapid growth assume the form of delicate threads. The thickening and stiffening of these delicate threads complete the growth of the hairs.

The hairs do not arise over the whole surface of the crest at once, but each cell as soon as ripe for the effort puts forth the capillary process. The further development of the canals and labyrinth our author describes in the following words: —

"Ohne dass die äussere Gestalt der Blase in irgend einer Weise geändert wird, beginnt an der lateralen Wand des Organs und zwar an dem dorsalwärts gelegenen Abschnitt derselben eine Gewebsmasse sich dergestalt anzuhäufen, dass sie vom Epithel bedeckt als mehr weniger breiter Streifen oder Wulst von aussen oben in die Blase hereinragt. Diese Substanzanhäufung oder Wandverdickung, wie ich mich zunächet vorurtheilslos ausdrücken will, hat beim Häring eine länglich ovale Form, bei den Salmoniden dagegen tritt sie von vorn herein in exquisit dreizipfeliger Gestalt (Fig. 4) auf und zwar verstreichen 2 zipfel nach dem vorderen und hinteren Ende der äusseren Blasenwand, der dritte Zipfel verläuft über die Mitte der dorsalen Wand. Schon früh zeigt dieser Wulst an drei Stellen ein besonderes Dickenwachsthum. So kommt es, dass schon bald die freie epithelbedeckte in das Lumen der Blase einragende Fläche nicht mehr glatt und eben erscheint, sondern dass sich auf dem schon im Allgemeinen erhöhten Terrain gleichsam drei besondere Hügel bilden. Diese besonderen Hügel entstehen immer auf den Breitseiten der dreizipfeligen Figur (bei den Salmoniden). Es muss daher entstehen ein vorderer, ein hinterer und ein unterer Wulst. (Fig. 6 w. 7: *W. v, W. h, W. w.*) Dieselben sind nun auch gerichtet nach vorne,

hinten, unten, alle drei zugleich mit einer mehr weniger starken Neigung[3] nach der medialen Wand zu. Noch ehe diese Hügelbildung an der äusseren Blasenwand über die ersten Spuren des Entstehens gediehen ist, haben sich diesen späteren Stümpfen gegenüber an drei verschiedenen Stellen ganz gleichartige, nur viel kleinere Wülste (Gegenwülste, Fig. 5–7: *G. W. v*, *G. W. h*, *G. W. w*) erhoben, welche schon früh das Bestreben zeigen den genannten Stümpfen der aussen oben entstandenen Bildung entgegenzuwachsen. Zwei dieser kleineren Wülste, entspringen von den medianwärtsgelegenen Partien der vorderen und hinteren Blasenwand, der dritte entsteht auf dem Grunde der Blase zwischen der an dem Uebergang zur Aussenwand gelegenen Crista acustica und der in Nachbarschaft der Chorda dorsalis gelegenen Macula acustica mit ihren Otolithen (Fig. 8). *Aus dieser Stellung der Wülste geht hervor, dass immer je ein selbständig entstehender und ein je aus der gemeinsamen, an der äusseren Wand entstandenen Substanzanhäufung sich abgrenzender Stumpf die Tendenz haben, sich entgegenzuwachsen und gerade über je eine Crista acustica hinweg sich zu vereinigen. Das geschieht in der That* (cf. Fig. 8)." [Italics mine.] "Einmal angelegt nehmen namentlich bei dem Häring diese Wülste rasch an Grösse zu; die erst hügelartig vortretenden Bildungen haben beim Häring schon nach wenigen Stunden mehr fingerförmige Gestalt angenommen. Bis zur Vereinigung der Stümpfe zu vollständigen Balken vergehen beim Häring dann noch circa 24 Stunden." There could not be a more complete agreement between two developmental processes, occurring in different animals, than there is between the formation of the canals on the surface of the body in Amia and the formation of the canals of the internal ear in the Herring and Salmon as given by von Noorden. Of the correctness of the account for the latter I am certain, for I have observed the same process both in the whole embryo and serial sections. From our present knowledge of the development of the labyrinth in the bony fishes we have only agreement with the type of growth of the surface organs.

"Die Wülste verdanken ihre Entstehung der Anhäufung einer nahezu homogenen nur von einzelnen dichteren Streifen (Lamellen) durchzogenen Masse, welche eingeschoben ist zwischen Epithel und Bindegewebe, d. h. diese ganze Masse

ist anatomisch gleichwertig der Basalmembran, einem Ausscheidungs-produkt epithelialer Zellen."

In these words von Noorden distinctly shows that he has utterly failed to grasp the significance of the formation of the primary and secondary folds, and the histological differentiation which he looks upon as the cause of the canal formation is certainly only a secondary matter, a concomitant of the erection of the folds.

The further development of the labyrinth is brought about by the continuous growth of the arches formed in the manner described above into broad sheets, which convert the archways into canals. It is important to note that von Noorden found in a majority of cases that the two processes uniting to form the posterior canal usually came together last, though he thinks he has observed this pair to unite first of the three, and he concludes that there is no regularity in the process, especially as he had oftentimes observed the right and left capsules to be in widely separated stages of development, the right labyrinth being much more advanced than the left. The portion of the canal first formed is its ampulla, since the folds first meet over the sense organ or crista. We shall see later on that this fact has an important bearing on the solution of the difficult problem of the origin of the part in question in the higher forms, — the mammals especially.

The size of the processes forming the rudimentary canals varies considerably in the different species, but there are no fundamental variations in the relations of the parts.

The Development of the Ear in the Amphibia.

In the Frog the early history of the auditory vesicle is in all essentials, save one, a repetition of the development as given for the Shark. The exceptional condition is that the auditory vesicle develops entirely from the nervous layer of the ectoderm, and is always closed over by the epidermal layer. The endolymphatic duct consequently never opens on the surface of the head. This condition is retained by all the Sauropsida, and is certainly a secondary modification of the developmental process.

According to Villy (1890, 281), who has recently worked out the early stages of the development of the ear in the Frog very

carefully: "The earliest stage at which the auditory involution can be readily recognized occurs soon after the closure of the neural groove in the fore part of the embryo." It may be recognized as a perfectly distinct though shallow invagination, lined by a columnar epithelium belonging exclusively to the nervous layer of the ectoderm. At first the edge of the saucer is nearly circular, but soon becomes irregular and narrowed as the saucer is converted into the flask condition. Van Bambeke has figured and described these stages for *Pelobates fuscus*, and these two amphibious forms agree very closely in the details of the process. In sections Villy claims to have traced the auditory nerve into continuity with the somewhat thickened plate of cells before it has commenced the formation of the saucer. The flask stage is not so perfect as in the Elasmobranchs, and does not long persist, as the mouth of the involution is soon closed and the auditory vesicle loses its connection with the nervous layer of the ectoderm. Villy was not able to describe from his study of this process the details of the closing of the mouth of the flask with exactness, and there remains still some doubt as to the completeness of the closure. This dorsal region or neck of the flask is much smaller than the ventral portion and becomes ultimately the recessus labyrinthi. Villy says (*loc. cit.* p. 525): "The outer wall of the vesicle, being the latest formed, consists of cells at first indistinct in outline, but soon they assume, more or less completely, the columnar character of the opposite wall, though the two parts never agree exactly, as the older contains more pigment than the younger. It is from the old pigmented parts that the sensory tracts of the adult ear are formed." The cells of the older part are also more elongated than the others. The vesicle now becomes surrounded by the mesoblast in the usual manner. By the time the larvæ have grown to the length of 12–14 mm., the canals begin to appear, but already a separation has been effected between the two parts of the sensory patch, and thus the two chambers of the ear are marked off. They are the utriculus and sacculus, and this part of the ear is now in the Cyclostome stage of development. The appearance of the utriculo-saccular partition belongs to the stage of development when the animal has reached a length of about 11 mm. This partition first appears as a ridge, which by broadening finally divides the auditory

vesicle into an upper, inner, anterior chamber, — the utriculus, and lower, outer, posterior chamber, — the sacculus.

When fully formed this partition runs obliquely across the auditory vesicle, and as the ear approaches its adult conditions, grows more and more oblique to the original axis of the vesicle. The semicircular canals of the Frog form, in the manner already described, for the surface canals in Amia and the auditory canals of the Elasmobranchs and Teleosts.

Relative to the time of appearance there are variations worthy of mention. The anterior and the external canals develop simultaneously, while the posterior is perfected only later. Nevertheless, the sense organ of the latter canal is cut off from the macula sacculi *before those of the anterior and external canals are formed.* Villy adopts the view that, on account of the later development of canalis posterioris, the older idea that the two vertical canals are older structures is not correct. The posterior canal appears before the folds of the other canals have united, and it forms exactly like the others. The two vertical canals continue to grow until they meet and their two half-pores unite into a primary pore, which opens on the inner surface of the utriculo-sacculus. On account of the late appearance of the posterior canal, Villy unfortunately concluded that the deduction from the comparative anatomical evidence bearing on the case, which holds the Cyclostome ear to be an ancestral structure, from which the Gnathostome vertebrates have derived their auditory organ, to have insufficient foundation; and he says (*loc. cit.* p. 529), "This doctrine is very much shaken by the results arrived at in this paper." Villy distinctly says that the early appearance of the sense organ cannot be considered as showing that the posterior canal forms first. In this view he shows that he has totally failed to appreciate the significance of the relation existing between the sense organ and its canal.

Our author says (p. 532): "The fact that this epithelial tract is the first to develop might be taken to show that though the posterior vertical canal actually forms later than the others, nevertheless it is indicated earlier than they are. This early specialization may, however, possibly be explained as a convenience due to the out-of-the-way position occupied by the organ concerned, and to the early formation of the septum between the utriculus and sacculus, which in its growth plays

an important part in separating this patch from the rest. Besides, I do not think that the time of specialization of the sensory tracts of the ampullæ is a safe guide to the relative times of evolution of the canals, as there is no rule of development common to all three. If the ampullæ were actually homologous structures, and their development had not been interfered with, they would form in the same way; but as they do not do so, it is safer to assume that the original course of development has been modified, than that the ampullæ are not homologous. This would seem to show that the order of the evolution of these epithelial patches has not been preserved."

The sensory epithelium invaginated into the vesicle covers the whole length of the floor, at the time of the appearance of the utriculo-saccular septum, and passes up on to the inner wall. It also laps over the anterior, lower, outer angle of the utriculus. The sensory epithelium passes without sharp demarcation into the remaining pavement epithelium of the utriculus. As already described, the utriculo-saccular septum divides this patch into two, from the posterior of which the macula sacculi and the crista acustica posterioris is budded off. Soon after this the macula utriculi buds off a single small patch, which soon divides into the cristæ acusticæ anterioris and horizontalis. The macula sacculi lengthens, but for a long time remains continuous with its bud, the cochlear organ. The lagena appears early after the formation of the canals. The endolymphatic duct grows out from the utriculo-saccular wall, and makes its way into the cranial cavity, early establishing the relations characterizing it in the adult. The manner of the division of the cochlear sense organ into pars basilaris and lagena is not thoroughly understood; and I have not been able from my preparations to decide whether it arises from the macula sacculi or from the papilla lagenæ. Villy erroneously includes the macula neglecta, *i.e.* macula abortiva, in his list of cochlear sense organs: as I have shown elsewhere, it really belongs to the sense organ of the posterior ampulla.

The Development of the Ear in Reptiles.

Hoffmann (1889[1]) has worked out the development of the parts of the ear in *Lacerta viridis*, and has confirmed Rathke's

[1] Bronn's *Klassen u. Ordnungen*, VII, 3, 1889.

account of the development in *Tropidonotus natrix*, to which he has added much in the way of detail.

After a very short account of the early transformation processes in Lacerta, in which Hoffmann merely confirms the prevalent ideas of the origin, mode of growth, and early relations of the auditory vesicle, he passes on to a more detailed account of the later transformations of the growing ear. He states (p. 2012) that the auditory vesicle rests on the large auditory facial ganglion as on a cushion, the inner face being covered by the ganglionic mass, which also reaches around onto the anterior, posterior, and ventral faces of the vesicle.

The auditory flask has been so displaced with reference to its original position that its originally relatively large opening, now very much reduced and on the verge of closure, appears as though pushed dorsad. After the closure of the external pore of the endolymphatic duct it remains for a time connected with the epidermis. The separation is finally completed, but only after the canals have begun to form, and the whole structure has been pushed ventrad to near its final position at the side of the medulla.

The closed endolymphatic duct reaches dorsad by a much narrowed portion quite to the ectoderm. This process is the recessus labyrinthi or aquæductus vestibuli of the authors.

Hoffmann observes that "Es scheint mir denn auch wohl nicht zweifelhaft, dass dieser Anhang oder dieser stielförmige Fortsatz dem langen, dünnen Rohr entspricht, welches bei den Selachiern das knorpelige Primordialcranium durchbohrt, dorsalwärts mit der Epidermis der Körperoberfläche in verbindung steht und dort eine offene Ausmündung besitzt, wo dem zufolge eine Verbindung des zum Labyrinth sich umwandelden Höhrbläschens mit der Körperoberflache dauernd fortbestehen bleibt," a conclusion justified by the facts of development and adult structure, not alone for the Reptilia, but as well for all other vertebrates in which the primitive endolymphatic duct closes early in development or appears only relatively late in ontogeny as an outgrowth of the utriculo-sacculus. In the latter case it is an atavistic phenomenon, and is an excellent illustration of the great degree of persistency of structures which, although no longer possessing important functions, at the same time do not in any way prevent the functional perfection of the organ or

endanger the life of the animal. Hoffmann's account of the differentiation of the ear sac is in harmony with the prevailing ideas, that the sac first divides into superior and inferior portions before the former gives rise to the canals and the adult utriculus, while the latter is converted into the adult sacculus (receiving the endolymphatic duct) and the cochlear tube. For his account of the development of the semicircular canals, he quotes Rathke's observations and applies them to Lacerta. The sensory epithelium soon makes its appearance by the growth in length of its cells and the formation of sensory hairs on the hair cells, and the distinction between sensory and non-sensory areas is still further increased by the flattening of the cells of the latter.

In respect to the nerve-end organs, he says (p. 2015): "Dadurch, dass das Gehöhrbläschen sich in die verschiedenen Abtheilungen sondert, wird auch das Höhrepithel in eben so viele einzelne Flecke zerlegt, zu denen sich dann der Nervus acusticus begiebt. Das Höhrepithel zerfällt mithin bekanntlich in: 1) Eine Macula acustica recessus utriculi; 2) eine Macula acustica sacculi; 3) eine Macula s. papilla acustica basilaris; 4) eine Macula s. papilla acustica lagenæ; 5) eine Macula acustica neglecta; 6, 7, 8) drei Maculæ s. cristæ acusticæ ampullarum."

Development in the Birds.

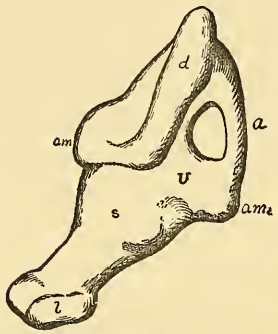
Although so many authors have studied the embryology of the Chick, no one seems to have followed the development of its auditory organ beyond the very earliest stage, and there are no observations known to me on the division of its sense organs. I have seen the sense organ which is invaginated before it has gone below the surface and while still in the saucer stage, but further than this I have not followed its development. His[1] (*loc. cit.* p. 107) says: "Jede Gehörblase erscheint als eine dem Nachhirn seitlich anliegende Grube, welche nach innen, nach vorn und nach hinten von einer scharfen, doppelten Contour umsäumt ist, während die äussere Gränze in unbestimmter Weise sich in die Seitenwande des Kopfes verliert. Ihr durchmesser beträgt zu der Zeit ca. 0.1 mm. Etwas früher sieht man in der Flächenansicht nur einen vierseitigen Flecken

[1] *Untersuch. u. d. Erste Anlage der Wirbelthiersleibes.* Leipzig, 1868.

von grösserem Umfang als die spätere Grube, und die Gränzen des Fleckens verlieren sich nach allen Seiten hin in ziemlich unbestimmter Weise." Balfour's observations do not go further than this, so that we must rely on the adult anatomy for our conclusions as to the probable course of development of the integral parts of the bird's ear. The structure of the adult internal ear of birds is so very similar to that of the reptilian type that there can be little doubt of the essential agreement of the phases of its development with those of the reptilian ear given above.

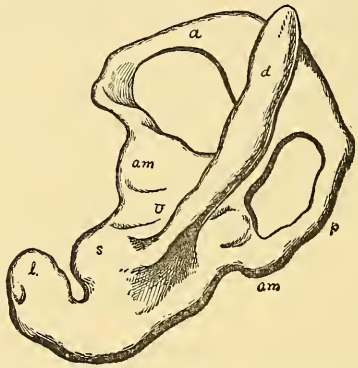
Development of the Ear in Mammals other than Man.

Krause, who has recently studied the development of the mammalian internal ear, finds that in the Pig and Sheep, when



Cut 21. — The ear of a very young Rabbit embryo, 11 mm. long. Figure after Krause.

a Anterior canal.
am Ampulla.
d Ductus endolymphaticus.
l Lagena.
s Sacculus.
u Utriculus.



Cut 22. — The internal ear of a somewhat older Pig embryo, 33 mm. long. Figure after Krause.

a Anterior canal.
am Ampulla.
d Ductus endolymphaticus.
l Lagena.
p Posterior canal.
s Sacculus.
u Utriculus.

fully cut off from the exterior (and this occurs in embryos 6 mm. long), the auditory vesicle forms a compressed sac, having an irregular quadrangular shape. The utricular and saccular divisions are readily distinguished, and already the semicircular canals have begun to differentiate by the formation of two shallow depressions in the wall of the utriculus (of authors) (Cut 21); both the pocket common to the vertical canals and

the pocket for the horizontal canal are present. Below the pocket for the horizontal canal is seen the larger and deeper evagination for the cochlea. When the embryo has reached a length of 8 mm., the cochlea has so far developed as to stand out distinctly from the sacculus, and is at the same time somewhat bent.

At both ends of the common pocket for the verticals, and at one end of the horizontal depressions, are slight enlargements, the future ampullæ. From now on the parts rapidly acquire individuality. The anterior canal is completed first, then the posterior, then the horizontal. The whole vesicle undergoes a marked change during this period, for owing to the growth of the ductus endolymphaticus from the utricular part and of the cochlear tube from the saccular division, the labyrinth has now the appearance of being extended in a dorso-ventral direction. The cochlear canal has now one-half turn, and a long groove has appeared on the inside of its wall (fold on the outside), from which the nerve-end organ, Corti's organ, arises.

In embryos of 30 mm. length the canals are all well formed, and the ampullæ prominent. The two verticals, which from their mode of development have up to this time occupied the same plane, now begin to diverge, and the planes of the canals now meet in the middle of the common arm which unites them. Their angle is 150°. This method of origin is most interesting and important in its bearing on the spatial relations of the adult ear canals. The cochlea has now nearly one spiral turn.

Krause failed to observe the separate formation and was in error with reference to the origin of the two canals — anterior and posterior verticals, from the fact that at the time when the evagination to form the *canals* has become well marked the two grooves have run together and hence appear as a single fold. The truth is that there are two ampullar depressions which give rise to outgrowing canals. These canals having their separate origins are to be regarded as distinct, though they fuse at so early a period.[1] Krause looks upon the resorption of the intervening tissue as a necessary step in the formation of the semicircular canals. Notwithstanding Krause's assertion that the ampullæ form at the same time as the canals, I am certain that the ampullar depressions make their appearance before

[1] See Recapitulation D.

the canals begin to form. This process is true of all forms yet studied with this matter in view.[1]

It is not my purpose to give at this time an exhaustive account of the development of the cochlea. All that I shall attempt to do here will be to present in essentials the condition of our knowledge as established by the investigations of Huschke, Remak, Reissner, Kölliker, Hensen, Middendorp, A. Rosenberg, Gottstein, Pritchard, and Retzius, and to give a short account of the few additional, but as I believe important, facts which I am able to add to our previous fund of knowledge, and to point out the modifications in the older views where these new facts seem to necessitate fundamental change in our conceptions of the pedigree of this organ and its present morphological significance.

The comparative ontogenetic history of this organ shows us conclusively that the cochlea was not created after a cut-and-dried plan, and having once been established among mammals has gone on serenely ever since reproducing itself; but, on the contrary, embryological evidence shows that there has been a struggle for existence among the parts of a growing organ, the struggle ending in the annihilation of the unsuccessful candidates for the privilege of existing. The antagonism began quite as soon as the original differentiation of parts took place, somewhere far back in the line of the sauropsid ancestral stock, and has continued ever since in that group. In the passage from Sauropsid to Mammal (the manner and the means of the accomplishment of the change are as yet hidden from us) there occurred a selection of the fittest (probably), which gives us the mammalian organ of Corti of the adult; but even to-day the unsuccessful candidates are developed in the young of *Man* as in all other mammals up to the functional perfection, so far as we may judge on the basis of the structure, only to

[1] The earliest account of the ontogeny of the cochlea is given by Ibsen, according to whose observations the cochlear canal is formed from the large otolith sac by the gradual recession of the otolith from the wall on which it lies (*i.e.* the inner wall carrying the sense organ). During its transition, it draws the wall of the chamber along with it, and by contact with the other side or wall of the chamber divides the tube into two scalæ, while the triangular (in section) canal left between them becomes Corti's canal. The nerve supply runs across in the partition thus formed. The otoliths have disappeared as such, having been converted into the lamina spiralis accessoria.

be reabsorbed, to fade away entirely as organs, soon after, leaving only the faintest traces of their previous strength and perfection of development; for, strange as it may seem, the apparently physically strongest organ is the one which disappears, leaving the smaller organ, which at the same time seems to have acquired a higher degree of cell differentiation, to occupy the field alone. The story of the "Rise and Fall" of organs, of cell communities, is repeated within the cochlea, nor is it by any means all told yet. The organ of Corti, as it exists to-day in the higher Mammalia and in Man, is in a state of flux; and although change in any direction is undoubtedly very slow, yet there is a tendency to increase in size and complexity very manifest in this structure. The present organ has a future before it; but annihilation will remove it out of the way for the better adapted successor among the future mammalian descendants, just as the sauropsid organ has disappeared before the present mammalian organ of Corti.

It took a long time and much study for the older investigators to arrive at correct conceptions of the relations of the cellular elements of the organ of Corti to the floor on which it rests, even in the adult ear. The Marquis Corti had only the faintest conception of the actual condition of the cellular elements in the organ discovered by him, and none, of the significance of the morphological relations of this cochlear organ to other parts of the ear. His original view was that the cells forming the organ followed one another in an even layer, much as in any layer of columnar epithelium. They were thus spread out evenly, he thought, on the basilar membrane, and this conception of the relation of the parts in the adult affected powerfully the ideas of its course of development.

Claudius (1855, 53) first saw that the arches of Corti raised the mass of the organ of Corti above the basilar membrane.

Boettcher (1856, 29) and Deiters (1859, 66), who worked little with cross-sections, thought the cells of Claudius followed directly on the hair cells without a break in the surface.

The structure called papilla spiralis by Huschke (1835, 148), and Organon Köllikeri by Hensen (1864, 127), formed that part of the epithelial thickening of the floor of the cochlear tube in which the whole of the auditory nerve was supposed by these earlier investigators to end. In this epithelial ridge, or papilla

acustica, as Hensen also called it, he found four kinds of cells —(*a*) rods, (*b*) hair cells, (*c*) elongate peripheral cells (supporting cells), (*d*) Corti's and Deiters's cells (Stäbchenzellen of Leydig, Haarzellen of Kölliker).

In tracing the development of these parts of the adult Corti's organ in the embryo, Hensen started with the epithelial ridge as the basis of all; and since in the adult a membrana tectoria had been described, he searched for it in the embryo, but could not find it; and, considering the methods then in vogue, one is not surprised at his lack of success.

Hensen concluded that the perforate membrana tectoria of the bird's ear was the *analogue* of the striated membrana of the mammal ear, and he considered both to be the product of the secretion of the cells of the epithelial ridge. By the growth of the basilar membrane and the lengthening of the rods of Corti, the papilla acustica, or that part of it which represents hair cells of the organ of Corti in the adult, was pushed out under the edge of the tectorial membrane, which by this time had separated from the surface which secreted it as a permanent gelatinous mass floating freely, except the attachment of its inner edge, in the endolymph above the short hairs of the hair cells.

The few facts given above were about all that had been obtained relative to the organ of Corti by the observers down to Boettcher's time.

Boettcher's great service consists in his having given us a very extended account of the development of the auditory apparatus in several species of mammals. The stages he studied were sufficiently close together to allow of tracing all the changes with certainty, and in this way his monograph contains the completest and most accurate account of the growth of the mammalian internal ear of any author down to this time; for Retzius's studies of the development in the Rabbit, Cat, and Man may fairly be considered to be contributions to Boettcher's exposition of the ontogenesis of the mammal ear, as I think the author himself considered them. Retzius confined his embryological studies almost entirely to the ontogeny of the cochlear duct.

According to Boettcher (31, 1869) the cochlear tube arises as a bulb-like pocket from the sacculus, and soon turns inwards and

forwards, growing in the direction indicated by this spiral twist; *i.e.* downwards, forwards, and outwards. The cochlear ganglion accompanies it with its nerve cells in intimate contact with the columnar epithelial cells of the thickened floor of the canal. *All these parts, nervous and sensory, develop consecutively from the base to the apex by interstitial as well as apical growth.* There is an interstitial increase in length, due to increase in size of the elements composing the organ, and new elements are added throughout the growing organ. The apical portion is always much younger and more immature than the other parts, as, for example, in an 8.5 cm. Sheep embryo the cochlea has made two and one-half turns. The scalæ tympani and vestibuli are beginning to develop. The apical end of Corti's organ is in the epithelial ridge stage, while the basal part of the cochlea has already developed its rods, hair cells, and other structures characteristic of the adult condition.

In cross-section the cochlear tube is at first flat, with a slit-shaped lumen, but the canal soon enlarges and becomes irregularly oval, the shape of the outline of the cross-section varying in different parts of the canal in any given period of growth.

There is a great difference in thickness between the epithelium of the floor and roof of the canal in the embryo without sharp separation from the side walls, but this character is greater in adults, when also the separation of the thickened floor from the walls becomes more evident. The epithelial ridges, as they grow, become separated by a distinct groove between them.

At this stage (Pl. III, Fig. 1) the organ has reached very nearly its mature condition as regards the presence of the essential features of its anatomy in the adult, but certain parts still remain which form the most positive evidence of its derivation from a more extensive and less specialized plate of sensory cells or macula acustica. This evidence is seen in the persistence of the primitive hair plate, and the division of the nerve supply between the Sauropsid organ remnant and Corti's organ. It may with appropriateness be called the saurian stage, owing to its great resemblance to the cochlear organ of the adult Alligator. In a transverse section of the cochlear organ of this stage, we have a repetition, part for part, of the Alligator's cochlear organ, and an essential agreement of the histological characters of the latter, although the mammal is born and is exercising its mam-

malian intuitions. The cochlear organ of the Alligator is not a genuine organ of Corti, but is the cochlear organ of the saurian type of reptilian ear developed along the line of histological differentiation laid down in the simpler members of the group. By this I do not wish to say that the saurian cochlear organ is the strict homologue of the macula acustica or papilla basilaris of the Amphibia and lower groups of reptiles.

The *inner hair cells* are well developed and are already separated from the outer hair cells, not only by the developing pillars of Corti, but also histologically by the appearance of individual characters which persist and are increased in later life. Some of these characters are, briefly, a different shape of cell body, different length of the hairs, a different relation to the nerve fibres and supporting cells, and to the basilar membrane and arch of Corti.

The main process met with in the transformation of the epithelium of the floor of the embryonic cochlear tube consists in the rapid increase in size and number of the cells along certain lines parallel with the long axis of the cochlea. There are two such ridges which need our special attention: I. The large epithelial ridge; II. The small epithelial ridge.

The *first*, or large, ridge begins near the habenula perforata, and extends outwards, covering about two-thirds of the basilar membrane in radial direction; on its outer slope it passes immediately into the

Second, or the small, ridge which extends outward, *i.e.* in transverse direction to about the beginning of the zona pectinata. It equals in length the large ridge, but is inferior in height and breadth.

According to Boettcher the whole of Corti's organ is developed from the small epithelial fold, while the large ridge gradually undergoes reduction until it disappears as a structure of the cochlear canal; its cells form the lining of the sulcus spiralis internus. The first cell of the small ridge develops into the inner hair cell. Boettcher holds that each inner hair cell is composed of *three* cells. The second cell of the small ridge develops into the pillars of Corti. The third cell of the small ridge develops in the first row of outer hair cells. The fourth cell of the small ridge develops in the second row of outer hair cells. The fifth cell of the small ridge develops in the third row of outer hair

cells. The sixth cell of the small ridge develops in the fourth row of outer hair cells.

Gottstein, however, concluded that in the Dog the last cell of the large ridge developed into the inner hair cell, and that the nerve fibres, which enter the habenula perforata, must necessarily force their way upward through the cells of this ridge, since they cover over the openings. The nerve fibres become connected with the cells of the large ridge which undergo atrophy, and later on are reduced to the so-called granular cells (Körnershicht, Gottstein).

The sulcus internus arises by the growth of the basilar membrane between the inner edge of the large ridge and of the crista spiralis, and not alone by the disappearance of the mass of the ridge itself, as Boettcher believed.

The cells forming the acoustic apparatus outside the outer hair cells in Man, Boettcher supposed were derived from the zona pectinata. Hensen called them supporting cells, while Gottstein was inclined to look upon them as being the remaining cells of the small ridge which had not reached a full development. He speaks of three rows of hair cells for mammals other than Man, and of four rows for Man as developing out of these cells. The evidences which led him to this conclusion were the similarity in the rounding off of the embryonic and adult ridges, and the presence in Man of a greater number of rows of hair cells than is present in most mammals (the latter statement has been shown by Retzius to be incorrect, and as my own preparations show, the Pig, Cat, Ox, and Man have equally the four, and even five, rows of hair cells of the external group), and the presence along the outer border of the membrana reticularis of additional elements beyond the region of the hair cells.

The inner hair cells were first well figured by Deiters, but Boettcher claims to have discovered them. He says (*loc. cit.* p. 94) with reference to the hairs borne by these cells: "Wie aus meinen Untersuchungen hervorgeht sind die Haare oder Stäbchen, welche an der Oberfläche sowohl dieser innern, als auch der später zu nennenden äussern Haar-oder Stäbchenzellen an vielen Präparaten sichtbar sind, künstlich durch Abreissen der Corti'schen Membran erzeugt. Ich habe mich daher aus diesem Grunde veranlasst gesehen beide Namen zu verwerfen."

According to Boettcher, the hair cells at first are simple, but

later on they acquire two nuclei, and then divide transversely, in each case producing an upper or surface hair cell and a lower or buried auditory cell, which is not hair-bearing. The former is Boettcher's "absteigende Hörzelle," which is fixed to the membrana reticulata, in whose separate existence Boettcher fully believed, while the latter cells were called by him the "aufsteigenden Hörzellen" or supporting cells, and were fixed to the basilar membrane. Their most rapid development takes place about the time of birth. In some animals it begins before birth, but in the majority the impulse to special growth is not received until after they come into the air. The cells then begin to elongate rapidly and soon divide. Their protoplasm acquires a complication of structure not yet fully worked out, and only partially understood. Boettcher found that in hair cells immersed in aqueous humor there was to be seen only a transparent protoplasm evenly but finely granular, but in cells killed in other reagents this transparent protoplasm was shown to possess a very complicated structure. My observations on the continuity of the capillo-nuclear fibres in the adult cells were made before I had seen Boettcher's paper, and his observations are the only ones in the literature of the subject which give us any details of the development of these fibres. These cells contain a glass-clear central fibre or cord which incloses the cell nucleus, and is itself inclosed in a very delicate pale sheath. Henle, the only other observer who has noticed this, supposed it was due to coagulation by HCl; but Boettcher has shown that most reagents produce it. Boettcher thinks that a similar process occurs in both rods and cells to produce these fibres, which he considers perhaps identical. This *central thread passes directly into the thread from the membrana tectoria.* When all the rest of the cell is destroyed, one sees it as a naked bundle of fibrils united to the nucleus.

Although the cells of the large epithelial ridge are resorbed without having shown the tendency to change their shapes or sizes, the cells of the small epithelial ridge early undergo a series of changes which transform them into the organ of Corti. The row of cells lying in contact with the outer border of the large epithelial ridge are changed into the row of inner hair cells (they are from a very early period hair-bearing cells), and bear long, strong hairs of the kind described in a preceding

paragraph. The nuclei of these cells lie near their upper ends, and their lower ends are in contact in any case with the nerve fibres: no actual penetration was observed.

The outer hair cells are similar in histological characters; they are, however, longer, and at first rise nearly perpendicularly from the basilar membrane. On account of the fact that they are further away from the entrance of the nerve, the fibres reach the cells only after passing across the intervening space by threading their way among the cells forming this part of the organ. The nerve fibres appear to end on the sides as well as the bases of these cells.

Kölliker (1867, 167) was the first to give us information on the development of the rods of Corti. He says, in his *Gewebelehre* (4th ed., 1863, p. 709; 5th ed., 1867, p. 727), in describing the growth of the organ of Corti: "Die erste Zelle erhebt sich unmittelbar nach aussen von den Löchern der H. perforata auf breiter dreieckiger kernhaltiger Grundfläche und ist mit ihrem in der Seitenansicht verschmälerten Ende stark schief nach aussen gerichtet. Die zweite Zelle kehrt sich mit dem schmälern freien Ende gegen die erste und wendet die breitere kernhaltige Grundfläche nach aussen. Diese beiden Zellen halte ich für die äussere und innere Corti'sche Fasern die jetzt noch ganz steil stehen, später aber mit ihren Grundflächen auseinanderrücken, was von einem Längenwachsthum der Zellen selbst, mit Verschiebung ihrer Basis, oder ihrer Grundlage, der M.b., abhängen kann." Hensen and Middendorp both were convinced that each rod rises from a single cell, but for the rest agree with Kölliker. Boettcher found, on the contrary, that both rods rise from one cell, which by longitudinal division separates into the two rod cells. After a detailed account (of which Retzius's II gives a good excerpt), Boettcher says (*loc. cit.* p. 85): "Der ganze Entwicklungsvorgang, durch welchen die Stäbchen sich bilden, ist als Theilungsprocess einer Zelle aufzufassen. Aus jeder Hälfte geht ein Stäbchen mit der ihm zugehörigen Bodenzellen hervor. Das Stäbchen und die Bodenzellen bilden ein Ganzes und sind als eine einzige Zelle zu betrachten, deren Substanz sich zum grössten Theil in feine Fasern verwandelt hat, während, nur ein kleiner Rest am Boden und im Winkel des Stäbchens in seiner ursprünglichen Beschaffenheit sich erhält. Es ist daher nicht richtig, diesen allein für sich als besondere

Zelle (Bodenzelle) hinzustellen; er gehört zum Stäbchen, wie auch Kölliker behauptet hat und wie ich noch genauer für erwachsene Individuen nachweisen will."

From my own observations I am confident that division begins below and works upward into the heads. In some cases, these never become completely separated, and thus is given firmer union to the two elements of the arch of Corti. The undivided part is in all cases only the cell wall which incloses the fibres of Corti's rods.

The view which all previous authors have held with reference to the nature and origin of the membrana tectoria (so-called) is that this structure was a cell secretion and was poured out by and upon the upper ends of the cells forming the surface of the organ of Corti. Boettcher, however, more consistent than other observers, maintained that this was the only product of the cell activity, while others claimed that besides the membrana tectoria the cells, by a process unknown, or similar, produced the short rod-like structures known as auditory hairs (Gehörstäbschen). These hairs were supposed to be formed in such a way that they projected into the membrana tectoria's substance in holes either preformed or produced by the growth of the hairs into it.

According to Boettcher's observations on the Sheep (and my preparations of the Pig confirm his statements so far as the time of appearance of the hair band is concerned) the first trace of this structure is to be seen in the 5.5 mm. embryo. The epithelial ridges are not yet distinctly formed, and the membrana tectoria simply lies over the thickest part of the floor as a thin *radiately striated* plate.

After working over preserved material without satisfactory results, Boettcher says (*loc. cit.* p. 123): "Auch an der mit Vorsicht in Humor aqueus isolirten Corti'schen Haut lässt sich kein befriedigendes Resultat über die ganze Ausdehnung derselben gewinnen. Sie erscheint weich, aber in hohem Grade elastisch. Der dünnere hyaline und der dickere streifige Theil können durch eine längsverlaufende Linie nicht gegeneinander abgegrenzt werden. An den Schnitträndern nimmt man gewöhnlich nur ein seichtes Abschwellen und dann wieder ein Anschwellen der streifigen Zone wahr, bevor sie mit leicht abgerundetem Rande aufhört."

Boettcher describes this structure as he found it in the 15 cm.

Calf and the four-week-old Cat in the following words: "Die Corti'sche Haut steht demnach sowohl mit den obern innern Hörzellen, als auch mit den äussern absteigenden Hörzellen (den drei Corti'schen Zellenreihen) in Zusammenhang, indem an die obere Endfläche jeder dieser Zellen ein faseriger Fortsatz ansetzt. Ob er weiter in die Zellen eindringe, oder blos mit ihrer Endfläche oder mit den ihren obern Rand umschliessenden Ringen sich vereinige, kann nicht entschieden werden."

"Dieser Umstand erklärt die an denselben bekannten haarartigen Fortsätze oder Stäbchen, nach denen sie benannt worden (Haarzellen, Stäbchenzellen). Die Haare oder Stäbchen sind Kunstproducte die durch das Abreissen der Corti'schen Membran entstehen. Geschieht dieses, so lösst sich der mit der Endfläche der betreffenden Zellen zusammenhängende verhältnissmässig dicke und scheinbar solide Fortsatz in eine Anzahl feiner Fortsätze auf, die in Verbindung mit der Zelle wie an ihrer Oberfläche befindliche Cilien erscheinen. Diese existiren aber in Wirklichkeit nicht. Es ist daher auch die Bezeichnung der Zellen als Haarzellen oder Stäbchenzellen ungerechtfertigt."

After detailing Kölliker's observations, with which our author formerly agreed, and according to which the membrana tectoria arose as a cuticular secretion, first from the large epithelial ridge and later from the small epithelial ridge, Boettcher says (*loc. cit.* p. 137): "Ob aber die Corti'sche membran als eine 'Ausscheidung' dieser Zellen auftritt scheint mir doch fraglich.

"Ich habe lange der Auffassung Kölliker's Beifall gezollt, dann machten sich aber Zweifel geltend, die ich noch nicht überwunden habe. Veranlassung giebt mir dazu eine Beobachtung, die sich mir an Durchschnitten embryonaler Schnecken sehr häufig und immer in derselben Weise darbot. Ich finde an Präparaten, an denen die Corti'sche Membran abgefallen ist, nicht nur dass aus den inneren und den absteigenden äusseren Hörzellen (innere und aussere Haarzellen Kölliker's) haarartige Fortsätze sich erheben, welche ungewöhnlich fein und lang sind und in dieser Beziehung den bei ältern Thieren an ihnen beobachteten scheinbaren Cilienbesatz übertreffen, sonden auch dass aus den obern Enden der hohen cylindrischen Zellen des grossen Epithelialwulstes ebensolche haarartige Fortsätze hervorragen, die meist eine bedeutende Länge erreichen. Diese

Fortsätze wachsen unzweifelhaft aus den Zellen heraus; die des grossen Epithelialwulstes scheinen mir eine Richtung nach aussen, die des kleinen nach oben und innen einzuschlagen. Auf diese Weise treten sie einander entgegen und wäre eine Aneinanderlagerung resp. Vereinigung derselben möglich. Es liegt daher der Gedanke nicht fern, die ganze Corti'sche Membran als die Summe der von den Cylinderzellen hervortretenden feinen Fasern oder haarartigen Fortsätze zu betrachten.

"Wie diese mit einander sich verbinden, um eine zusammen hängende Membran zu bilden, vermag ich nicht zu sagen; vielleicht findet gleichzeitig auch eine Ausscheidung aus den Zellen statt.

"Sehr bedeutungsvoll für die ganze Sache erscheint mir, dass auch bei erwachsenen Thieren eine Zerlegung der Corti'schen Haut in feinste Fibrillen möglich ist."

It will be remembered that Kölliker maintained that there were no fibres in the membrana tectoria; it being on the contrary a strictly homogeneous cuticular mass, while Hensen, on the other hand, described distinct fibres and a "Zwischensubstanz" as the component parts of the tectorial plate.

Regarding the structure originally described by Loewenberg as lying like a net upon the surface of the membrana tectoria or the hair band, Boettcher says he never found Loewenberg's net as Henle had described it, nor could he find any such structure as Hensen had described as forming a constituent part of the tectorial superstructures of Corti's organ. The development of the net was not determined with certainty, but was supposed to be the result of the impress of neighboring cell-heads upon the surface of the growing membrana tectoria, or at least its free surface layer.

The observations made by our author upon another of the little-understood structures, the so-called membrana reticulata, enabled him to make a valuable addition to our knowledge of Corti's organ. His observations have not, however, received deserved acceptance from the anatomists of the times (*loc. cit.* p. 139): "Wenn ich die Membrana reticularis wie üblich hier noch als ein besonderes Gebilde aufführe so mag es dadurch entschuldigt werden, das diese durchbrochene Lamelle nach ihrer Trennung von der Membrana Corti einerseits und von den unter ihr befindlichen Zellen andererseits eine gewisse Selbst-

ständigkeit zu besitzen scheint und durch die Eigenthümlichkeit ihres Baues das Interesse in hohem Grade in Anspruch nimmt. Sie ist jedoch kein einheitliches Gebilde, insofern an ihrer Zusammensetzung ganz verscheidene Formelemente Antheil haben."

Boettcher never saw Deiters's transverse nerve fibres in the cochlea, which are equivalent to Kölliker's longitudinal system of cochlear nerves. He thus criticises the view (p. 169): "Abgesehen davon ist ihr Vorkommen zwischen den Bogenfasern, wie schon E. Rosenberg, angegeben hat, mit der Entwicklung dieser nicht gut vereinbar und was die longitudinalen Züge betrifft, welche weiter nach aussen zwischen den äusseren absteigenden Hörzellen verlaufen sollen, so ist auch deren Existenz aus theoretischen Gründen zu bestreiten, weil der Raum zwischen ihnen von den aufsteigenden Zellen ganz ausgefüllt ist."

Pritchard (1878, 217) gives the following account of the development of the organ of Corti. Outside of the group of long cells which fill the sulcus spiralis in the embryo there lie five somewhat shorter cells (his primary cells), of which No. 1 (counting from in, outwards) divides itself transversely into 2. Nos. 3, 4, 5 acquire two nuclei each by the division of the parent nucleus. The outer four (2, 3, 4, 5) form the four hair cells of the outer rows from their upper parts, and the Deiters cells of their lower parts. From each Corti's cell shoots up a process which later splits into the hairs. Cell No. 2 becomes more triangular (in perpendicular section of the organ) by the broadening of its base. Its nucleus grows and divides between the two; a vacuole appears in the common protoplasm — the rudimentary tunnel. The lateral walls of the cell (*i.e.* inner and outer walls) have developed into the rods of Corti. The membrana reticularis originates out of the union of the upper ends of the primitive cylindrical epithelial cells. In the same way that the walls of these cells develop into the trabeculæ or perpendicular fibres which stretch from the membrana reticularis, to the membrana basilaris, and are homologous with the Müllerian fibres of the retina. Pritchard concludes that Corti's arches, the trabeculæ, the membrana reticularis, develop out of the walls of the primitive epithelium, the hair cells out of the cell contents, while the membrana tectoria is a secretion from them. The views here expressed show that this author did not

add anything to the facts already discovered by the German anatomists. In the following paragraphs I give the main features of the cochlear ontogeny of the Rabbit as given by Retzius, with whom I agree, except in the cases noted further on.

Development of Rabbit's Ductus Cochlearis.

1. *In the Embryo.*

The papilla acustica basilaris develops in the first ten days after birth — *i.e.* it acquires its maturity, and for the main part ends its development during this time. From the beginning on the canal is strongly depressed on its vestibular side. The ductus cochlearis consequently forms throughout most of the embryonic life a flattened epithelial tube whose walls are composed of cylindrical cells, the whole tube being inclosed in connective tissue (the so-called mucous tissue or Schleimgewebe of the Germans). At first there is no distinction to be noted in the structure of its walls. The floor, or neural wall, however, thickens early, and soon thereafter develops the so-called epithelial ridges. The manner of growth of the organ has not been satisfactorily made out, but the organ of Corti, as well as the tube, grows progressively away from the basal portion. Interstitial growth is certainly not proven to occur.

Retzius found the first trace of Corti's pillars and their inner neighbor cells to reach upward from the basilar membrane as *two* triangular cells whose bases are below, while their narrowly truncate upper *ends lie in border angle between the* large and small folds or epithelial ridges.

Just within from these occur the inner hair cells already laid down and provided with hairs. These cells, then, belong to the *larger fold*, and are placed in its outer border. The direction of these cells is, as in the adult animal, oblique from below and within upward and outward. The three rows of outer cells lie without the pillars and belong to the smaller epithelial fold. They are already in the embryo, *i.e.* before birth, laid down as hair-bearing cells in all of the spires. They are bottle-shaped, granular cells, carrying their nuclei in the lower parts of their cells. Their hairs are short and more or less perpendicular. The hairs of the third row are slightly inclined inward and upward.

The supporting, or Deiters's, cells project upwards among the hair cells from their broad basilar ends, and end pointedly be-

tween the cells at the surface of the papilla. They stand nearly perpendicularly upon the basilar membrane, and at this stage resemble the pillar cells in shape and histological features.

The membrana tectoria lies upon the limbus spiralis and the larger epithelial fold, and sometimes may be seen to reach as far as the rows of the outer hair cells, though usually its edge is found (especially in osmic and chromic acid preparations) over the inner hair cells, thus leaving the outer hair cells and the rows of pillar cells uncovered.

The nervus cochlearis varies in its relations to the cochlea with the increasing spiral twisting, which bends the ganglion more and more, and thus displaces the cochlear fibres. The fibres at this stage are mostly non-medullated, and are not to be traced beyond their entrance into the sense organ except with difficulty.

2. *In the New Born.*

The large epithelial fold of the papilla acustica basilaris is not raised from the wall of the ductus cochlearis. Its curved surface declines gradually inwards, where it passes at an obtuse angle into the surface of the small epithelial fold. The very long cells of the large epithelial fold incline inwards within, stand perpendicularly in the middle, and incline outwards in the outer part of the sense organ.

Corti's pillars grow larger and broader very rapidly after birth. They form two closely placed cell rows, which, however, are completely separate and disunited. Their nuclei are large and lie at bases of cells. The tunnel has not made its appearance between them.

The inner and outer hair cells are somewhat larger than in the embryo; otherwise they are the same as before birth. The histological features of the cell protoplasm in the adult have not yet begun to make their appearance.

The membrana tectoria covers with its thicker portion the large epithelial ridge, lying very close to the surface, and passing over (as yet there is no trace of sulcus spiralis internus) the large ridge, hangs free over the outer and inner hair cells, sending fibrous prolongations to the hair cells of the papilla acustica basilaris; but these processes are not in any way connected with the hairs of the hair cells; on the contrary, the latter pro-

ject freely between the processes. In later stages of development it is demonstrable that these processes are fixed to the upper end plates of Deiters's cells, *i.e.* the phalanges.

In the basal and middle spires the lamina spiralis is much more developed than in the apical, and the peculiar transformation of the large ridge has begun, the cells of the ridge disappear from within outwards, their places being taken by cubical epithelial cells. By this means a split appears between the membrana tectoria and the epithelial surface, which grows progressively towards the cochlear apex. The large ridge is highest in the apical turn, and is at this time in the height of its development.

The inner hair cells lie more inclined outwards than before and have increased in size, at the same time taking on more of the adult appearance.

The pillar cells are in a very interesting stage of their development. In the apical turn they are closely placed and do not show signs of separation. They are both inclined outwards; they have grown much in radial breadth, especially the inner pillar, which has sent a process of its foot quite to the habenula perforata. In the middle turn they have grown more than in the apical spire. The inner cell has grown the most, and traces of the head have formed, and the tunnel has made its appearance as a narrow split between the cells, about the middle of their length, just above the spiral bundle of nerve fibres. In the basal turn the tunnel is much better developed and the pillars of Corti are nearer their adult condition, for the pillar fibres have appeared in the cells as a clear refractive stripe. The inner hair cells have a different inclination for each turn of the cochlea, and their disposition is shared by the cells of Deiters. Hensen's supporting cells are fewer in the basal turn than in the middle turn, where they are most numerous. The nerves are better developed than in the last stage, they having gained in number and in amount of medullated tissue. The membrana tectoria is as in previous stage. It is connected by the processes from its outer zone with the Deiters cells, and the hairs of the hair cells project freely upward between the processes. The vas spirale is disappearing, while the basilar membrane is growing broader and becoming more like the adult in the character of its fibres.

3. *In the Rabbit One Week Old.*

The large epithelial ridge is disappearing in the apical turn, and it is much reduced elsewhere. The membrana tectoria lies only on the crown of the large ridge, and a space has appeared between it and the epithelial surface which becomes the sulcus spiralis internus.

The pillar cells have developed their pillars and separated from each other, forming the tunnel, except at the very apex of the cochlea. Nuel's space is now more fully developed than at any previous time, and is relatively as well developed as in the adult. Hensen's supporting cells have developed and they form the highest part of the small ridge, which appears much larger than the now much reduced large ridge. Hensen's supporting cells are best developed in the middle turn at this stage.

The membrana tectoria reaches outward to a point above the outer hair cells, and its outer zone has grown thicker. In the apical turn it hardly reaches to the second row, whereas its fibrous processes reach downwards to the Deiters cells, as before described. In the middle and basal turns these fibres are broken off, and one finds only remnants preserved in their attachment to the hair cells.

4. *In the Ten Days Embryo.*

The organ of Corti is now nearly complete. All that remains of the large epithelial ridge is the inner supporting cells, and they are lower now than those of the small ridge, which forms the highest part of the papilla acustica basilaris. The pillar cells are almost fully developed. The tunnel of Corti and Nuel's spaces are fully developed, as are also the inner and outer hair cells, and they have taken their adult positions. Hensen's body is to be seen near the upper end of the outer hair cells. Deiters's cells have grown much longer and carried the nerve end cells upward. The membrana tectoria reaches to the outer hair cell row and shows traces of the broken fixation fibres present in earlier condition, partly on the upper ends of the third row of Deiters's cells, and partly on the border of the membrane itself. The vas spirale is recognizable by the reduced rudiments of its walls.

By the fourteenth day the cochlea of the young Rabbit has

reached its permanent condition, and in the main subsequent changes affect its size only.

The Boettcher cells, which are developed in the bottom of the sulcus spiralis externus, are simply the undeveloped remainder of the low epithelial ridge which formerly occupied this region. They disappear after the first month.

There is no difficulty in harmonizing Retzius's story of cochlear ontogeny with the views which I have sufficiently set forth in preceding pages, when it is remembered that he has described the appearance *en masse* of the sensory hairs, the whole membrana tectoria as a unit, not having recognized the individual hairs. The same is true of the spiral nerve fibres.

Hensen showed by measurements on the Ox the amount of translation of these structures during development, and found that the inner cells travelled quite up to the habenula perforata, while the outer row remained (with exception of the apical cells) practically in the same position. Hensen considered this spreading or diverging of the pillars of Corti as a process by means of which the hair cells of the small ridge were transported under the membrana Cortii. Middendorp concurred in this view. Boettcher found that the pillar structures moved *outwards*. In the adult the space between the feet of the pillars *decreases* continually from above downward, while in the embryo the space between the feet of the pillars *increases* continuously from above downwards.

The inner pillar is at first longer than the outer, then for a time they are of equal size, but soon the outer pillar grows longer and remains so ever after.

Hensen in 1873 again took up the subject and concluded that the translation of the papilla from without, under the membrana tectoria, was fully proven in the case of the Ox.

In embryos the pillars are perpendicular and close together. The upper end of the arch is inclined outwards.

Retzius further studied the development of the cochlea in the Cat, selecting the following stages: embryos of 8, 12, and 15 cm. in length, and the new-born fœtus, for the embryonic or early development, and the three-days, seven, eleven, and thirty-days old Kittens. He found the development essentially the same as the Rabbit, with the exception that the new-born Cat is much farther advanced than the new-born Rabbit.

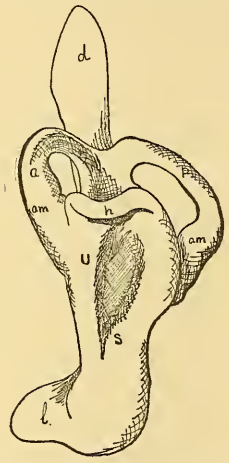
The Development of the Ear in Man.

In embryos three and a half to four weeks of development the internal ear consists of the slightly laterally compressed auditory vesicle, from the dorso-median portion of which the recessus utriculi has become well marked off. With the exception of the crista of the post. ampulla, all the nerve end organs are at this time laid down in the extensive union of the acoustic nerve with the anterior wall of the auditory vesicle.

The medial ganglion of the VIII nerve supplies the sacculus and cochlear region. It is the saccular branch.

The lateral ganglion of the VIII nerve supplies the utriculus, the ampullæ (external and anterior). It is the utricular branch.

Up to about four and a half weeks the human ear retains the form of a hollow sac provided with a hollow stalk (Cut 23). After this period the division of the originally simple cavity into two nearly equal parts gradually becomes more and more distinct, and here, as in other mammals, the sacculus is from the first devoted to the production of an extensive cochlea, so that almost before it is formed its ventral region is bent and moulded into the cochlear pocket, whose growth from this time on is rapid in a ventral direction, spirally along a dorso-ventral line. The anterior and posterior divisions of the auditory vesicle, owing to the twisting of the nerve and revolution of the vesicle, no longer lie along an antero-posterior axis, but move nearly the one above the other along a vertical axis, so that they are commonly described as the upper and lower chambers of the ear. The two divisions of the auditory ganglion belong exclusively to their respective auditory chambers, and as the separation progresses a median raphe springs into the vesicle cavity much as it is seen to do in the adult Myxine and especially Petromyzon (utriculo-saccular septum).



Cut 23. — The left internal ear from a human embryo, 13 mm. long, about the fifth week of development. After W. His, Jr.

a Anterior canal.
am Ampulla.
d Ductus endolymphaticus.
h External canal.
l Lagena.
p Posterior canal.
s Sacculus.
u Utriculus.

About the fifth week the parts of the adult ear are all well marked out. The two primary canals, anterior and posterior verticals, inclose between them an angle of 160° and open into the utriculo-sacculus by a short common tube, while all three present the S-shaped curvings so characteristic of the canals in many fishes. The horizontal canal remains still a shallow groove in the utricular wall.

The nerve end organs of the utriculus lie very close together, and at this time one cannot distinguish separate nerve branches. The fibres of the utricular branch spring from the whole surface of the utricular ganglion and pass in the form of a loose bundle to the inner face of the utriculus, its sense organ having divided. The fold has appeared in the cochlea, which later development proves to be the beginning of the organ of Corti, *i.e.* the forerunner and parent organ.

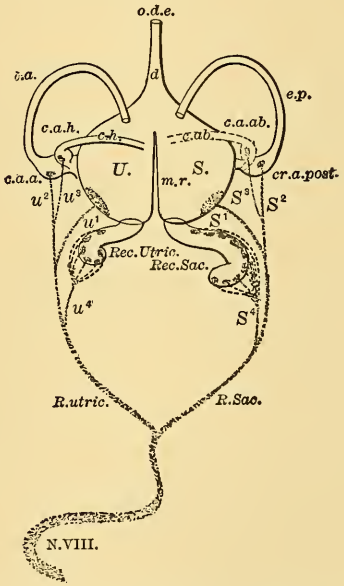
About the second month the parts of the internal ear have assumed their adult condition, with the exception of the epithelial sensory end cells, which have not as yet been perfected, though very distinctly modified from the remaining cells of the ampullæ and utriculus and sacculus. The canals and ampullæ are well formed, and each canal has a well-developed ama. The ama of the external canal is the only one to persist in the adult. The utriculus and sacculus are connected only by the split endolymphatic duct, *i.e.* by the divided surface canal, and the cochlea has nearly separated from the sacculus, retaining only the slender canalis reuniens as a tubular communication. The cochlea is at this time spirally twisted one and a half turns, the most important change in the form of the canal since the last stage.

The trunk of the acoustic nerve lies very closely applied to the anterior wall of the auditory capsule (excepting the aquæductus vestibuli). One cannot find a layer of mesoderm cells between the ear capsule in Man. This antero-mesial portion of the ear capsule contains the entire amount of the thickened epithelial plate that later is to form the nerve end apparatus of the adult internal ear, and consequently all these parts are held to have direct relations to the auditory ganglion at this stage. The posterior semicircular canal forms an exception to this, for it receives its nerve supply at a relatively late period of life. His was unable to find a nerve branch running to the posterior ampulla earlier than the sixth week. This condition of things

recalls the entirely similar method of development, described by Villy, for the Frog, a member of the Ichthyopsida. Here, however, the canal itself does not develop until after the anterior and horizontal canals have made their appearance, so that the conditions of development are even more modified.

When judged on the basis of the adult conditions found in the members of the mammalian group, the *ontogenetic* development of the cochlear tube progresses much more rapidly than the differentiation of the sense organs contained. Phylogenetically the organ of Corti is well developed before the tube has made its first spiral turn; *i.e.* while still in the Sauropsidan condition, as exemplified in Echidna and Ornithorhynchus, but ontogenetically this is not the case; for in the ears of the embryos of Man, Ox, Pig, Rabbit, Mouse, and Cat, the organ has scarcely begun its histological differentiation at the time when the adult condition, as regards number and form of the spiral turns of the cochlear tube, has been attained.

Mainly on account of the great development of the brain in the human species more than in any other Mammal, and the consequent altered relations of the cranial bones, the vertical axis of the lower vertebrate ear is shoved to one side, so that in Man, for example, it is directed from within, below, and in front — outwards, upwards, and backwards. In keeping with this change is the alteration in the direction of the horizontal axis of the lower vertebrate ear, so that in Mammals it comes to nearly coincide with the vertical axis; in other words, there has been a revolution of the ear on two of its axes, the main change having taken place by a revolution of nearly 90° in the plane of the vertical axis.



Cut 24. — See explanation of Pl. IX, Fig. 3.

The nerve end organs of the human ear are six in number.

1. Macula acustica recessus utriculi.
2. Crista acustica ampullæ anterioris.
3. Crista acustica ampullæ externalis.
4. Crista acustica ampullæ posterioris.
5. Macula acustica sacculi.
6. The mammalian cochlear organ, or Corti's organ.

The two nerve end organs possessed by most all Vertebrates from the fish up to Mammals are thus seen to be wanting in these latter, — viz. macula acustica neglecta and papilla acustica lagenæ cochleæ,[1] — while the important sense organ of the cochlea of Saurians has disappeared in the adult, though fully developed in the embryo, and functionally perfected before the completion of Corti's organ, which supplants it.

E. Phylogenetic Considerations.

"Ich sagte, es sei mir gelungen, einen Grundplan des Gehörorganes der Wirbelthiere, das Wesen des Baues desselben festzustellen. Dieser einfache Plan muss nun nach dem grossen in die Wissenschaft eingeführten Principe wenigstens annäherungsweise am meisten in der niedersten Wirbelthierclasse hervortreten und sich zugleich auf das strengste an die jüngsten Entwicklungsformen des Organes bei den Wirbelthieren überhaupt anschliessen" (Hasse, 1873).

After an examination of all the evidence bearing on this question, both from the embryological and the anatomical sides, I propose the following solution of the problem of the morphological value of the parts of the internal ear and their interrelationships. I believe there can be no doubt that the internal ear develops from superficial canal organs, and this belief has led me to the discovery of the very simple law which governs their origin and succession. Stated in few words their origin and sequential relations are as follows: —

The primitive auditory sense organ is invaginated from the surface of the body, and may be said at this time to be in the vesicular stage (Cut 25, *A*). So far as we know, this condition is not retained by any adult living vertebrate. And it is quite possible that the auditory saucer may contain the rudiments of

[1] The papilla acustica basilaris has also disappeared as such, and is represented by only one of its descendants, the organ of Corti.

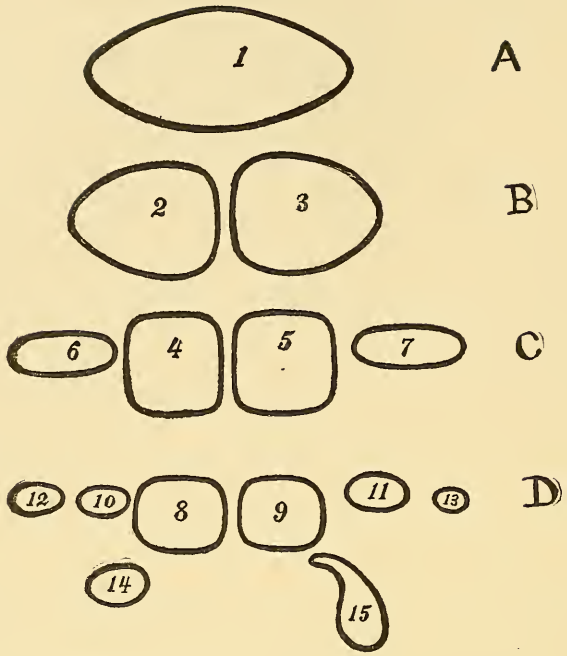
the two primary sense organs of the Cyclostome ear. The parent sense organ soon divides transversely into two nearly equal parts, which are the anterior and posterior sense organs respectively. The auditory vesicle is at the same time partly separated into two chambers (incomplete canals) to accommodate them. These chambers are the utriculus and sacculus.

Each of the two sense organs of the second generation after a while divides into two unequal parts in such a manner that the smaller sense organ appears as a bud from the parent. There are thus formed within the two chambers of the ear four canal sense organs belonging to the third generation. The two external organs are soon inclosed within the ampulla of two complete and relatively large canals, which are now formed about them, — an anterior vertical and a posterior vertical, formed in the manner already fully described. Up to this time the organs have retained the primitive relations to each other — a serial arrangement along a line running in an antero-posterior direction. Now there begins a distortion of the structure as a whole, which continues ever after, and reaches its greatest development in the Mammals; viz. a process of sinking and drawing out ventrally of the posterior chamber of the ear, so that hereafter we might speak of a superior chamber and an inferior chamber. The sense organs of the third generation play the leading *rôle* in these changes, and by means of four sets of divisions, viz. by the bipartition of each sense organ present in the Cyclostome stage nearly simultaneously, there is produced a fourth generation of canal sense organs.

To this fourth generation belong all the sense organs of the internal ear of the higher vertebrates which in the diagram are numbered 8 to 15 consecutively.

During this process of sense-organ differentiation, the canals have been variously modified, and to show the relationship of the third generation to the fourth let us examine the diagrams shown in Pl. IX, Figs. 2 and 3, in the construction of which I have ignored the ventral distortion spoken of (Cut 25).

The sense organ numbered 6 in the Cyclostome stage (the crista acustica anterior, or anterior canal organ, of Myxine and Petromyzon) has divided to produce sense organs 10 and 12 of the Gnathostome stage, *i.e.* the cristæ acusticæ anterioris et horizontalis, of the human ear.



A Auditory vesicle.
B Utriculo-sacculus.
C Utricular sacculus + two ampullary canals.
D Utriculo-sacculus + two ampullary canals and lagenar canal.

Cut 25. — Stage A represents the undivided superficial sense organ of the vertebrate ancestor, as it is invaginated from the surface and inclosed within the auditory vesicle to function as the macula acustica vesiculi; the only auditory sense organ of this stage. It is but little removed from the canal organs as they exist in, *e.g.* Amia, and differs from it mainly in size. This condition is not represented in the adult of living Vertebrates.

Stage B represents the first division of the macula vesiculi, into its two offspring, the maculæ acusticæ utriculi et sacculi. This stage is likewise not represented among living forms.

Stage C is so characteristic of the Cyclostomata, so far as we know them, that we will call it the Cyclostome stage. Here the cristæ acusticæ anterioris et posterioris have made their appearance.

Stage D shows the condition of the organs in the Gnathostomata, hence its name, the Gnathostome stage. The cristæ acusticæ anteriores, horizontales, posteriores, and abortivæ are all developed by the division of the two parent ampullary organs of the Cyclostome ancestral stage, while the maculæ utriculi et sacculi undergo division, giving rise to the parents of the utricular and saccular complexes of sense organs. These latter reach their highest differentiation in some Rodentia and porcine species.

The sense organ numbered 4 of the Cyclostome stage (the macula utriculi of Myxine and Petromyzon) divides into the sense organ 8 and sense organ complex 14 of the Gnathostome stage, the macula utriculi of the human ear, which is, as I stated when describing the Torpedo ear, a compound organ composed of the parent organ and its numerous progeny, all of which remain close together.

The sense organ numbered 7 of the Cyclostome stage is the sense organ of the posterior canal of Myxine and Petromyzon, and has divided to produce sense organs 11 and 13 of the Gnathostome stage, or the crista acustica posterioris, or the canal sense organs of the posterior canal of the human ear, and the so-called macula acustica neglecta of Retzius, which is the abortive second horizontal canal organ of the internal ear of man.

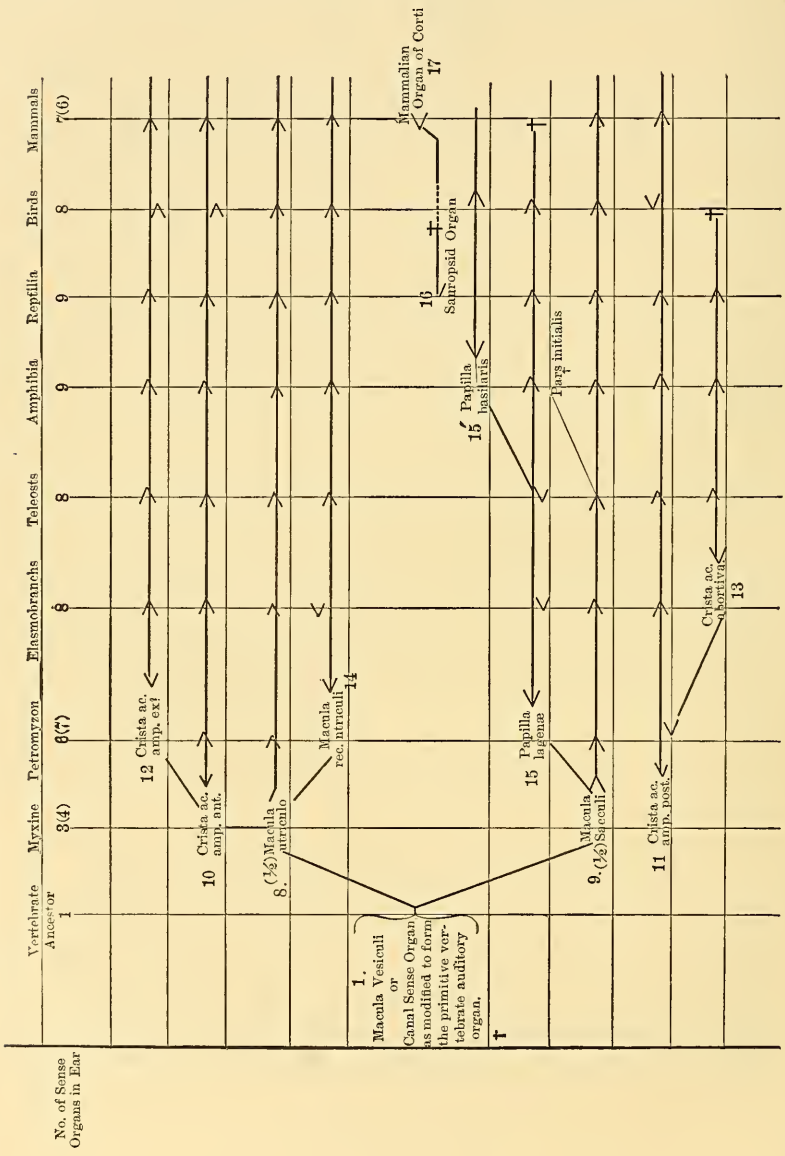
Sense organ 5 of the Cyclostome stage has divided to produce the sense organ 9, and the sense organ complex 15 of the Gnathostome stage, or the macula sacculi and the lagenar organ respectively, the organ of Corti of the human ear.

With the exception of the generalization that the vertebrate internal ear is derived from branchial sense organs — *i.e.* organs of the lateral line system — a generalization which we owe to Beard, but which he did not attempt to establish by any detailed anatomica or embryological investigations, the phylogenesis of the vertebrate ear has been studied only on the basis of the adult structure.[1] Such structures as the semicircular canals and the divisions of the body of the auditory vesicle have been used alone as the basis for proofs of the genetic connection of the types of internal ear — even the nerve supply has been excluded from its just share in forming the conclusions generally accepted hitherto.

The following table gives the genetic relation of the several sense organs of the ear, the group of animals in which each organ made its appearance, the length of time it persisted or whether it still persists, measured in terms of geological time, the fluctuations undergone by organs during their term of existence, whether of increase or decrease, and the time of death together with the group suffering such loss. In the case of the papilla basilaris, although it rises in the Reptilia into the

[1] See Recapitulation D.

form of the Sauropsid organ, it is only among the higher members of the class of Saurians that it is found, while among the birds the organ is not so fully differentiated as it is in the Saurians, and it is not intended to show by the diagram that the Sauropsid organ increases in value or is even present in birds in such perfection as it exists in the higher Reptilia.



Retzius finally came to the conclusion that this nerve end organ had arisen from the posterior, ampullar sense organ, and that among the higher forms, especially the Mammalia, it was no longer produced, or, as he expressed it, the macula neglecta in these forms had disappeared in the crista acustica posterior.

These canal structures had no special phylogenetic significance for investigators in this field; for although it was known that the auditory vesicle was invaginated from the surface of the body, the connection of the sensory part of the invagination with the superficial canal organs was not understood. Now that we know that there is a genetic connection, many of the intricate problems receive their solutions, and the genetic relationships appear clear and certain for all the types. The demonstration of these facts deals another blow, and a fatal one, at the degeneration hypothesis which has been so persistently applied to the elucidation of Cyclostome anatomy and development, with such pernicious morphological results. (This will apply equally to Amphioxus, though only indirectly in this particular instance.) This solution relieves us from the necessity of explaining away the vertebrate ear on every occasion, when we seek to establish a relationship between the vertebrate and the invertebrate types; for we are led to see the value of very simple, superficial sense organs in an undifferentiated group of animals, for the building up of structures of great complexity, and of intricate relations to other parts of the animal body in the members of higher forms, and also to recognize the manner in which the structure and functions of organs may be profoundly changed in the course of time. And it also enables us to understand how a primitive central nervous system like that of Amphioxus may be altered by the development, the high specialization of circumscribed areas of the periphery necessitating specialization of the central apparatus.

Now, while it is not known that Amphioxus is provided with an organ of hearing, the next higher forms do possess an internal ear of such structure that not only does it help us to understand the more complex Gnathostome type, but proves conclusively that, so far as the ear is concerned, the Cyclostomes have not suffered degradation of structure. In his paper on the development of Petromyzon, Scott (1887, 259), *loc. cit.* p. 297, says: "It is a question as to whether these pecu-

liarities are to be regarded as primitive or as the result of degeneration. The much greater simplification of the ear in Myxine suggests strongly of degeneracy, but, on the other hand, the entire absence of the horizontal semicircular canal may very well be a primitive feature. It is plain that the auditory organ of the Lamprey is derived from the same primitive type as that of the higher vertebrates; but whether in the differentiation of the Lamprey it has passed through stages higher than the present condition, and more like that of the typical fishes, cannot from present evidence be decided."

"Regarded as a whole, the sense organs of Petromyzon do not show degeneracy, but rather a retardation of development." As this quotation shows, Scott was well satisfied from his studies of the development of the Lamprey that it could not have descended from more highly organized ancestors, but he was not able to decide what relationship (to descend to particulars) the ear of Myxine bears to that of Petromyzon, nor the genetic connections of the Cyclostome ear with the higher fish type.

Scott's conclusion (*loc. cit.* 300) that "the epidermal sense organs of the head and the lateral line are not developed in connection with the ganglia of the cerebral nerves, or with the lateral nerves, but at a later stage" has been shown by Kupffer to be erroneous. And the light which the latter's researches have thrown upon the relation of the superficial sense organs to ganglion formation on the one hand, and to the internal ear on the other hand, is most welcome and important.

The walls of auditory vesicle are converted only in part into the labyrinth of the ear, the other part forming a ganglion; and since the relations of the invaginations in connection with the ganglia of the V and X nerves bear the same relation to these ganglia that the auditory involution does to the acusticofacial ganglia, and since we know the latter to be an involution of an organ of the lateral line system of canal organs, it follows that all these invaginations are intimately connected with production of the sense organs of this system. That the canals are not found in the Cyclostomes, save in the case of the auditory organs, is due to a secondary modification of the process of development; the process of canal formation going no further than the primitive invagination, which soon disappears.

Kupffer's objection that, in the case of the V and X ganglia, he was unable to detect anything like a sensory epithelium is hardly valid; for, in the case of the auditory vesicle, a relatively long period elapses after it is invaginated before it forms the isolated sensory epithelial patches; and considering that the V and X (auct.) do supply the sense organs of the lateral line throughout their territory, we cannot hesitate to accept such important testimony for its full value. Kupffer calls attention to the fact that these structures have the following things in common. First, they arise from a common Anlage. Second, they arise in the same horizon in the dorsal region of the body. Third, they have fundamentally the same mode of formation. Fourth, they have the same relations to the dorsal roots of their respective nerves.

Relative to the kinship between Cyclostomes and Gnathostomes, I quote Gegenbaur's opinion as expressed in a notice of Retzius's work (98, 1885) p. 127:—

"Von grossem Interesse ist es, zu sehen, wie die jeweilige Organisationsstufe des Labyrinthes im Wesentlichen mit der übrigen Organisation harmonirt, indem sie innerhalb einer gewissen Grenze sich hält. Unsere Vorstellungen von der Phylogenie der Wirbelthiere finden damit eine neue Bestätigung. So stellen sich die Cyclostomen von den übrigen Vertebraten, den Gnathostomen — so weit entfernt dass nicht einmal deren Bogengänge eine strenge Vergleichung mit denen des letzteren zulassen. Dieses bestätigt nur die grosse Bedenklichkeit der Schlüsse, die von der Organisation der Cyclostomen auf jene der Gnathostomen ohne Weiteres gezogen zu werden pflegen." It is not the least service which the anatomical facts brought together here have rendered, that they have proved that so far as the ear is concerned there is a direct relation between these two groups of animals, and that the former stand as the ancestors of the Gnathostomes. Whence, instead of rendering the phylogeny of the Gnathostomes more difficult, and isolating the Cyclostomes into unknown relations, the facts of auditory anatomy so far as yet worked out indicate the contrary in a very instructive manner. As we now know their auditory anatomy, the differences between Myxine and Petromyzon are in many respects as great as between Petromyzon and the fishes, and yet the two former undoubtedly belong to the same

group, which, so far as existing forms are concerned, is a very small one.

With the Elasmobranchs appear the third canal organ and its canal, the so-called horizontal, external or lateral canal. We know from the development that its sense organ arose by the division of the crista acustica ampullæ anterioris of the Cyclostome type. We are also in position to say that the older view advocated by morphologists, that the two verticals are the older, and the horizontal the younger canal, is the true one, while the view advanced recently by Villy is entirely erroneous — the reverse of the truth, and rests not upon a fundamental fact of development, but upon a variation, an ontogenetic departure from phylogenesis, such as not infrequently occurs in the development of all organs, especially in the higher animals.

Against the view that the completed canal of the canal system is the primitive condition of the system, so far as *existing* vertebrates are concerned, one may oppose the very plausible objection that, since all of the Holocephala and some Teleosts have the canal incomplete as a more or less open groove on the surface of the body, and since the Cyclostomes do not retain the canals in any form during adult life, and further, since the closed canal may be easily formed by the fusion of the borders of such open grooves as are present in, *e.g.* Chimæra, and Tetrodon, it is only reasonable to suppose that the *open groove* is the primitive condition and constitutes a phylogenetic stage passed through in the development of the higher type of closed canal. When, however, we consider that the internal ear is a *very ancient* structure, and that in all known cases the sense organs developed in it become inclosed in *complete* canals by a process exactly similar to that discovered in the formation of the sense organs and their canals in the admittedly primitive ganoid type, we are compelled to admit that such a process could hardly have arisen within the closed capsule after its separation from the surface and its removal away from external influences, and that consequently there must be a genetic relationship between the canal organs of the internal ear and the superficial canal organs; and since there is not the slightest doubt that the superficial canal organs are the original or parent organs, we are brought to the unavoidable conclusion that the vertebrate ear is a transformed canal organ. By the involution of the

auditory vesicle the organs are inclosed in a protecting vesicle, and a development of further *protective* structures would be, to say the least, a superfluity. If, then, the only rational view to take of the whole matter of the further differentiation and great complication of the auditory sense organ *after* inclosure necessitates the conclusion that all vertebrate forms possessing an internal ear, provided with canals and canal organs, must have descended from ancestors possessing a closed canal system on the surface of the body, I think that there is no escape from this conclusion, that the three distinct types of lateral line organs found in the Cyclostomes, the Elasmobranchs, and the Holocephala, Ganoids, Teleosts, and Amphibia are modified from the simple type of canal organs as they are still found in bony Ganoids, most Teleosts, and many of the Urodele Amphibia. As a somewhat parallel case where *intricate* structures are developed instead of the simple ones as had been supposed on *a priori* grounds to have preceded and led up to the formation of the complicated conditions, we have the phenomena of karyokinesis, or indirect cell division. It is now known that karyokinetic complications occur in the division of the unicellular forms of the organic world, and it would seem that direct cell division, whenever it occurs, is a shortening of the ancient and, so far as we can now see, original method of cell division. This view, as regards the homology of the canal organs in the several vertebrate groups, is the one which most recent writers who have dealt with the surface organs of the Ichthyopsida have advocated on the basis of very different facts from those which I have given here.

It follows from what has been said above that the system of canal sense organs is a very ancient one, since it must have antedated the origin of the internal ear of the Cyclostomes. For although absent from Amphioxus, it is proven to have existed in the Cyclostomes by the presence of the canal organs of the ear. The Cyclostomes do not now possess the canals during adult life, though there is good reason to believe that they are laid down in the young larvæ.

The Elasmobranch group shows many important and extensive modifications of this system in both the development and adult relations of these organs, and Balfour has pointed out the probable cause of the changes.

It is only among the Ganoids and their descendants the Teleosts that we get the most perfect preservation of the original mode of canal formation.

Although for the most part closed, Allis has shown (*loc. cit.* p. 491) that the lateral canal may for a part of its length remain an open groove.

Sagemehl's view, according to which the Teleost condition is derived directly from the Ganoid condition as typified in Amia, is, I believe, the correct view.

Balfour states (*loc. cit.* p. 445, II): "It is clear that the canal of the lateral line is secondary, as compared with the open groove of Chimæra or the segmentally arranged sense bulbs of young Teleostii; and it is also clear that the phylogenetic mode of formation of the canal consisted in the closure of a primitively open groove. The abbreviation of this process in the Elasmobranchii was probably acquired after the appearance of food-yolk in the egg, and the consequent disappearance of the free larval stage." Allis is evidently inclined to take the same view of the relation of these two forms of sense-organ channels, for he says (*loc. cit.* p. 530): "These different conditions both in the Teleosts and in the Ganoids would also be obtained if the development, as shown in Amia, was simply arrested instead of undergoing retrogression; that is, by supposing that the Teleosts had never attained the Amia condition, instead of having passed through it as indicated by Sagemehl." The modification in the development of the canals in Elasmobranchs is paralleled by the modified manner in which the auditory involution is formed in Amphibia and Teleosts, where the vesicle does not open on to the surface of the body in any stage of its growth, being formed as an involution of the nervous layer of the ectoderm in the Frog and in the Teleost as a solid ingrowth of this layer, in which the auditory cavity only later makes its appearance. Here we have an ancient structure lost from the ontogenetic history, and although an attempt to reproduce this structure is made by the embryonic cells, they are prevented by changed conditions. I think it cannot now be reasonably doubted that so far as existing forms are concerned *the closed canal preceded* all the various modifications which have been described.

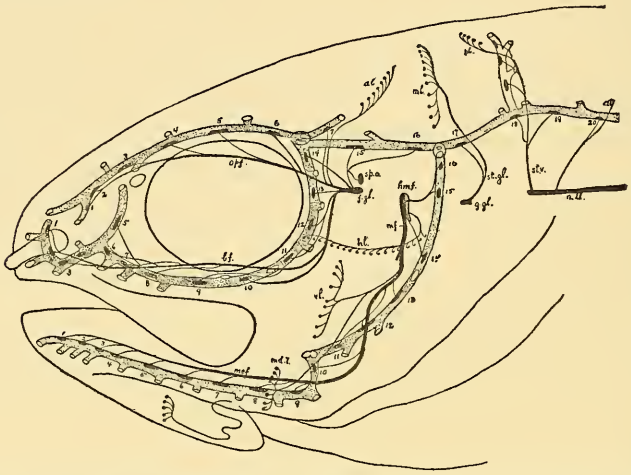
Why should the territory within the bounds of the superficial, common zone of the VII and IX have developed the ear? Why not some other part of the canal system?

Because plainly enough the sense organs in this zone were the most suitable structures for natural selection to seize hold of and develop further, both physiologically and morphologically, for the simple but sufficient reason that any sensory impulses striking this single region, so sharply circumscribed, would be propagated into two separated centres of the brain simultaneously, and thereby "ring in" a multiple alarm, and this single zone contained the only territory so provided. Owing to the peculiarities of the propagation of wave motion, one part of the head would have been as good for this as another, but it was necessary for the organs to be confined to small space. There exist in vertebrates to-day (most fishes and aquatic amphibia) similar arrangements which have been produced by the renewal of the sensory structures over the gap left by the insinking ear, and we thus have an incipient, superficial ear, which may in future, if the animals so provided should ever send up another growing stock capable of reaching the degree of differentiation represented by the descendants of ancient fishes, — the mammals of to-day, — I say this surface ear may be carried below and produce a second internal ear of the essential characteristics of the existing one. Animals higher than fishes have lost this potentiality, and are in danger of being compelled to give way to some new tribe of creatures which may sometime spring from the more generalized fishes armed with greater powers for the struggle of life, which may mean simply that they will be provided with more perfect sense organs.

We must not think of the fish type as a cold and fast, immutable thing, but as something plastic, in ceaseless agitation and strife toward greater perfection of organization, or in other words these vertebrates are still subject to the necessities of variation and survival of the fittest.

It is unnecessary to argue at great length to show that two neighboring sense organs receiving their nerve supply from two cranial nerves having distinct sets of central connections would be on this account specially suited to give the animal the greatest possible amount of information about what was going on outside, at the same time permitting the apparatus to occupy the least possible space. The ear Anlage was so placed that it might be housed inside the head, leaving the surface of the body free for sense organs of another degree of specialization.

No other area of equal size on any other part of the body could give the animal such good physiological service. Hence this area with its sense organs was specially suited to be differentiated by natural selection, and its early and sufficient involution and burial within the tissues of the head have ever since afforded protection to it, while all other organs of its kind have disappeared from the surface of terrestrial animals. The process of involution has enabled the animal to preserve primitive conditions — the necessary conditions of existence for such hair-bearing structures. Although the ear sense organs lie on the morphological surface of the body, yet they are kept immersed in a watery fluid.



Cut 26. — This diagram illustrates the relative position of the surface sense organs and their canals with their nerve connections in the Ganoid Dogfish. After Allis (4), Pl. XLII, Fig. 49.

The so-called semicircular canals develop as more or less curved structures, because they are formed out of a portion of the external surface of the body, which has been inclosed within the head. Since on the surface of the body, in the typical and usual process of development, the canals always open at both ends on the surface, so inside the auditory vesicle they open at both ends. Since they are laid down as curved grooves, they naturally hold that form as canals. The mechanical conditions of their development would alone cause them to assume the semicircular or curved shape. It must not be supposed that an

exact semicircular shape is the usual form of these canals, for such is far from being the case, and I have very great doubts that the mathematically accurate canal, or even a near approach to it, *ever* occurs in the whole vertebrate group. Usually the canals have the shape of segments of ellipses, parabolas, or hyperbolas ; when simple or when complex or irregular, a repetition of one or more of these curves. As has often been noted, the canals do not lie in the plane passing through the centre of the two ends and the centre of the middle portion (usually the apex) of the curve, but quite frequently one half the curve lies above, the other below, this plane. In man this is regularly so. In the bird the canals appear to be much more perfectly semicircular than in any other group save some of the fishes.

The canals do not even form about the same patch of sensory cells. For, according to some observations on the embryo fish and amphibian, the posterior canal originates about the cochlear patch of cells, while the anterior arises about a part of the utricular patch, the horizontal in its turn being formed by a division of the anterior sense organ. The adult ear preserves traces of this mode of development, as members of every vertebrate group whose anatomy has been studied clearly prove. In Myxine we have the simplest condition, the posterior canal, arising from the end of the vesicle opposite to the anterior canal, the former innervated by the cochlear, the latter by the vestibular branch of the auditory nerve. Between Myxine and the Elasmobranch the anterior canal organ divided, giving off the external canal organ. The saccular organ became separated from the utricular, but its offspring, the posterior canal organ, remained within the saccular territory. The cochlear organ, later, divides again. I have not yet worked out the full details of the development of the sensory patches of the ear above the fishes, but there can be no doubt that they all arise in the typical manner now known for the most important auditory sense organs. From the phylogenetic standpoint, then, the ear canals, both in their development and in their adult condition, certify to descent from surface canals ; or strictly speaking, they *conclusively show themselves to be the surface canals of a submerged superficial area, which, owing to its more or less flask-like form, permits only a mediate communication of its canals with the circumnatant fluid.* Even this communica-

tion is lost in most existing forms, and the inner surface of the ear chamber becomes the true mother surface of the ear canals.

One very important matter I have left over from the anatomical description, because a proper knowledge of the embryological stages is very necessary to its proper appreciation, indeed, for its demonstration. Ever since the discovery by Retzius of the "macula acustica neglecta" this auditory sense organ has been a source of discussion and investigation. Retzius, Hasse, Kuhn, and others have paid especial attention to it, and Retzius especially has investigated its occurrence and relations in numerous species of all the large groups of vertebrates. After giving the evidence he had gathered from such extended studies, Retzius sums up his researches and concludes as follows (*loc. cit.* p. 238): "Im Ganzen geht nur aus Obigem hervor, dass die fragliche Nervenendstelle weder, wie ich selbst für die Fische zuerst angenommen habe, die Pars basilaris cochleæ bildet, noch, wie Hasse und A. für die Amphibien meinten, einen, 'Anfangsteil der Schnecke' (Pars initialis Cochleæ) darstellt. Wir haben es hier hingegen mit einer ganz besonderen Bildung, einem eigenen und in der That sehr eigenthümlichen Endorgan zu thun, welches zuerst bei den Fischen auftretend bei den Amphibien, besonders den Anuren, seine höchste Entwickelung erfährt, bei den Reptilien wieder verkümmert, um bei den Vögeln und den Säugethieren *immer mehr zu verschwinden, gewissermassen in die Crista acustica der frontalen Ampulle, aus welcher sie moglicher Weise von Anfang an durch Abtrennung entstanden ist, zuletzt aufgehend.* Die bisherigen Namen dieser Nervenendstelle, sowohl Pars basilaris cochleæ als Pars initialis cochleæ, müssen also aufgegeben werden. Es ist nicht eben leicht, für sie einen guten neuen Namen zu finden. 'Macula acustica utriculi posterior' würde für die Meisten Fälle richtig sein, nicht aber für alle. Ich habe deswegen einen indifferenten Namen gewählt, und nenne nunmehr diese Endstelle 'Macula acustica neglecta' als Erinnerung des Uebersehens, welches ihr so lange Zeit zu Theil wurde." The sense organ thus described by Retzius is the product of the division of the posterior ampullar sense organ, as Retzius suspected on morphological grounds from his comparative studies of so many forms. The ontogeny of the organ in the Amphibia clearly proves its origin.

As regards the macula abortiva (macula neglecta, Retzius) in the Mammalia, there are two views; though there can be little doubt that Retzius is essentially correct in his conclusion that this sense organ has disappeared from the mammalian ear. Hasse objects to this view, on the ground that such important structures as sense organs, when once they have been fully formed, are not likely to disappear again; and since Henle and Reichert had described a small branch of the saccular nerve which they traced to what was supposed by them to be a small macula located in the sacculus near the dividing line between it and the utriculus, he concluded that the crista abortiva was really present in the mammalian ear. Retzius has more recently instituted a systematic search for this nerve branch and end organ in preparations of the human ear as well as in dissections of other mammalian ears made especially for this purpose, and has failed to find the slightest trace of such structures. He consequently concludes that the earlier observers were in error, and that *this sense organ has disappeared from the mammalian ear.*

Although I have shown that the crista abortiva is never a fully developed sense organ, being an abortive organ from its first appearance in the vertebrate series among the fishes until the waning powers of the parent organ fail to give birth to the organ at all (as in the mammalian group), it is not impossible that this sense organ may still occur in members of the lower mammalian groups, — *e.g.* the Monotremata, — or even that it may occasionally appear as an atavism in individuals of the higher orders. At the present time, however, we do not know of such instances, unless the observations of Henle and Reichert are correct. Admitting that such atavism may occur, Retzius's conclusion still remains essentially true. In either case the plan of the distribution of the nerves remains the same. It is evident from the history of this part of the ear that there is from the first a tendency toward the reduction of the parts first to appear in favor of the cochlear region, which steadily increases in functional importance and receives an ever-growing nerve supply. This nerve branchlet is not the only one which has disappeared during the transformation of the piscine into the mammalian ear; for we know of another branchlet occurring in forms as high as the reptiles which has ceased to be devel-

oped, and there may be still another. The one first mentioned is given off from the utricular nerve, while the second branchlet belongs to the saccular nerve.

The papilla lagenæ, which is so important in fishes, amphibia, reptiles, and birds, has disappeared from mammalian anatomy — disappeared in the same sense that the macula neglecta or crista abortiva has disappeared, by failing to appear in the development as a discrete sense organ. The Monotremes, it is true, are said to still retain the lagena, but they are hardly to be accepted as typical mammals. The subject receives added interest, however, from the fact of their still retaining the organ beside a genuine reptilian (saurian) cochlear organ. I think, by reviewing the matter in this light, that the views of Hasse and Retzius, apparently antagonistic, are made harmonious, and both are correct in the sense here indicated.

The new auditory sense organ, which the brothers Sarasin think to have discovered in the ear of *Ichthyophis glutinosus*, and which they propose to call the "macula fundi utriculi," is in all probability no other than the macula neglecta. I may say that Retzius's observations seem to me quite conclusive on this point. The spot is evidently an offspring of the saccular macula through the posterior canal organ, and so, in any case, belongs to the posterior division of the auditory chamber.

The proof is conclusive, I think, to show that Corti's organ is not, as Retzius supposed, the homologue of the papilla basilaris of the Ichthyopsida and Sauropsida, but only a descendant of this ancient organ. The differences of structure between the embryonic and adult cochlear organ in the mammals that have as yet been studied, are so great that we are justified in speaking of Corti's organ as an entirely new organ, which arose in the ear of the differentiating reptile in connection with those changes which produced the profound modifications of other organs of the body culminating in the mammalian type. The growth of the organ has been such that a fragment of the cochlear organ invisible to the unaided eye is sufficient to enable us to determine whether it was from a reptile, or a marsupial or placental mammal. The changes that have occurred in this organ in a microscopic way are then characteristic of what we commonly speak of as changes in type of structure as applied to gross anatomy, and they direct our attention to the fact that

deep-seated, *i.e.* thoroughly protected, organs are subjected to destructive changes in most unaccountable manner in correlation with changes affecting concomitantly all other parts of the body in greater or less degree. I must admit that it is by no means clear to me what has been the gain to mammals in changing from the sauropsid to the mammalian type of cochlear organ, for I can see no physical reasons why the reptilian organ should in great part be destroyed after having once acquired the degree of development it had attained in the immediate ancestors of the mammals and birds, as illustrated by the condition present in such a reptile as the Alligator.

Having found from my own investigations in three groups of birds, Rasores (Gallus), Columbinæ (Columba), and Passeres (Mimus), that the development of the cochlea is not so far advanced as in the hydrosaurian reptilia, it will be necessary to change the view advocated by Hasse, according to which the saurian reptilia stand as transitional forms between the amphibia and the lower reptilia and the birds, for it is obvious that in cochlear anatomy the birds hold a place apart from the direct line of descent as typified in the mammalian cochlea. As this is a matter of great importance, not alone as concerns the ear, but for the general problem of the phylogeny of the avian group as well, I quote the following account which our author gives of his views of the phylogenetic relationship of birds to reptiles as shown in the quotation from page 35 of his final digest of auditory anatomy.

"Das Gehörorgan der Crocodile bildet nun den unmittelbarsten Uebergang zu dem der Vögel, wie das von Siredon den schönsten Uebergang von den Fischen, namentlich den Teleostiern, zu dem der Amphibien zeigt und die Aehnlichkeit, namentlich in dem wichtigen Bestandtheile der Schnecke, ist so gross, wie sonst nirgends zwischen zwei Wirbelthierclassen, mit Ausnahme vielleicht zwischen Vögeln und Monotremen, welche letztere zu untersuchen ich leider keine Gelegenheit hatte. Ich finde, wie das überhaupt aus dem Verhalten der übrigen Organe bei den Vögeln zu erwarten, im Ganzen nur geringfügige Unterschiede in der Gestalt des häutigen Labyrinthes, die sich wohl dahin präcisiren lassen, das diejenigen Vögel, welche ein offines foramen rotundum besitzen (Natatores), also diejenigen, die wir als tiefer stehend erkannt haben, eine

relative kürzere, weniger entwickelte, schwächer gekrümmte Schnecke zeigen, als die mit geschlossenen (Grallatores, Columbæ, *e.g.*), und da die Schnecke gerade der Theil des Gehörorganes ist, der durch die Wirbelthierreihe hindurch allmählig immer höher sich ausbildet, niemals aber Rückschritte in der Entwicklung macht, so ist auch dieses Verhältniss für den Rang unter den Vögeln wichtig. Im übrigen begegnen wir hier wieder denselben Hauptbestandtheilen, wie bei den übrigen Wirbelthieren, der pars superior, dem eigentlichen Labyrinthe oder Bogenapparate und der pars inferior (sacculus und Schnecke), und beide besitzen an derselben Stelle, wie bei den übrigen Vertebraten, eine enge Communication in Gestalt einer engen, am äusseren Theile der Unterfläche der Vereinigung der Bogengangcommissur mit dem utriculus und der Verbindungsröhre der hinteren, alleinstehenden Ampulle befindlichen Röhre."

Hasse describes (118, p. 34) the morphological features of the Crocodile's cochlea (116, 1870) as determined by him, and, with little if any modification, what he says is true of the cochlea of the Mississippi Alligator. His statements are confined to the framework and cochlear walls and to the general form and features of this tube. As he does not describe the sense organs of the cochlea, I have endeavored to supply this want in a previous chapter. It should be borne in mind that this quotation really describes the *ancestral form* or type of the mammalian cochlear organ.

"Eine unendlich viel grössere Selbständigkeit bekommt die Schnecke, und namentlich die mächtig ausgewachsene *pars basilaris* gegenüber dem sacculus bei den Crocodilen. Die cochlea communicirt nicht länger mittelst einer einfachen Oeffnung mit dem hinteren unteren Theile des Sacklumen, sondern die Schnecke ist in allen ihren Theilen vollkommen von ihm abgeschnürt, die Verbindung der oberen Vereinigung der beiden Schneckenknorpel (Vorhofsblindsack) mit der Sackinnenwand, der membrana Reissneri mit der Sackaussenwand also vollkommen gelöst und nur indireckt vorhanden und zwar durch Vermittlung der communication, die zu einer vom hinteren unteren Theile des sacculus ausgehenden, horizontalen, nach aussen und etwas nach hinten gewandten Röhre, dem canalis reuniens, geworden ist, und die von jetzt an bei den Wirbelthieren als

constante Bildung auftritt. In diese gehen die Sackaussen-, -innen-, -ober- und -unterwand gleichmässig über, sich verdünnend, respective verdickend. Die Schnecke selbst, die bereits bei den übrigen Reptilien mit der Spitze, der lagena, eine leichte hakenförmige Biegung nach hinten zeigt, somit in der unteren Partie schwach nach vorne convex, nach hinten leicht concav ist, zeigt bei den Crocodilen diese Krümmung auf das deutlichste in der ganzen Ausdehnung, allein gleichzeitig eine spiralige Drehung (Halbspirale) und zwar derartig, dass wenn die membrana Reissneri, wie bei den übrigen Reptilien, in dem oberen Theile der Schnecke nach aussen sehend gedacht wird, sie an dem unteren mit der Aussenwand der lagena nach hinten sieht. Nun bekommt freilich die sichelförmig nach hinten unten gekrümmte Schnecke nicht diese so ausgeprägte, der der übrigen Reptilien entsprechende Stellung (membrana Reissneri aussen, membrana basilaris innen, Nervenknorpel vorne und viereckiger Knorpel, ligamentum spirale, hinten), sondern wegen der Krümmung des canalis reuniens statt nach hinten unten, nach aussen wird wenigstens der obere Theil der membrana basilaris nach aussen hinten, der untere mit der Innenwand der lagena gerade nach hinten gedreht, während dem entsprechend der obere Theil der membrana Reissneri, die hier als quergefaltete Membran, tegmentum vasculosum, erscheint, nach vorne innen, der untere mit der Aussenwand der lagena nach vorne gekehrt, wahrend der Nervenknorpel, der limbus spiralis cartilagineus wesentlich hinten innen, der dreieckige, das Spiral ligament, vorne aussen liegt. Die pars basilaris ist beträchtlich länger geworden dem entsprechend auch die Basilar membran. Diese ist aber auch relativ breiter, wie bei den Schildkröten und beginnt an der Einmündung des canalis reuniens, unterhalb dessen die Vereinigung der Knorpel zur Bildung der ersten Andeutung eines Vorhofsblindsackes vor sich geht, und endet an der lagena, die jedoch an Grösse nicht zugenommen hat. Gleichzeitig mit der Ausdehnung der pars basilaris und somit des Nervenknorpels hat dann auch natürlich die Ausdehnung des Nerven und der macula, die auch hier das anschliessende Drittel der Basilar membran einnimt, zugenommen, und diese setzt sich in die lagena fort, deren Nervgegenüber dem der pars basilaris jetzt selbständiger erscheint."

Keeping in mind the hydrosaurian type while examining the

mammalian cochlea, we shall have no trouble to follow the main phylogenetic steps of development of the latter, especially if we begin with the monotreme cochlea as the first mammalian stage.

I am in full agreement with Hasse's views of the relationships of the cochlea in the two groups as given below, except in so far as it relates to the lagena, where I am sure our author has fallen into a serious error in supposing that the lagena sense organ persists in the mammalia as a part of the organ of Corti. Of course he has not distinguished between the several derivatives of the primitive cochlear organ, and he consequently applies to the mammalian cochlear organ the old term, "papilla basilaris."

Hasse writes (118, p. 42): "Die beiden Knorpel würden also, wenn das Gehörorgan wie bei den niederen Reptilien senkrecht, statt von oben hinten nach unten vorne stände, wie bei ihnen vorne (limbus spiralis cartilagineus) und hinten (ligamentum spirale) liegen. Natürlich ändern sich wegen der ausgeprägten spiraligen Windungen der übrigen Theile des Schneckenrohres diese Lagerungsverhältnisse, doch sind diese leicht zu abstrahiren, so dass ich darauf keine Rücksicht zu nehmen brauche. Das sich die Schneckenröhre der Säuger und des Menschen in eine pars basilaris und in eine lagena theilt, brauche ich wohl kaum zu erwähnen, ebensowenig dass erstere vorzugsweise ausgewachsen ist. Die lagena hat sich dagegen nicht blos nicht fortgebildet, sie ist auch nicht einmal in ihrer Ausbildung stationär geblieben, sondern wir finden dieselbe einmal häutig geworden (häutiger Kuppelblindsack) und dann scheinbar reducirt. Sie ist hier nicht ampullenförmig erweitert, sondern stellt mehr das einfach blindgeschlossene Ende des cylindrischen Schneckenrohres dar.

"Die pars basilaris bildet auch bei den Saugern und Menschen, wie bereits angedeutet, einen Knorpelrahmen mit einem anfänglich vorne oben gelegenen Nervenknorpel oder limbus spiralis cartilagineus und einem hinteren, unteren, dreieckigen, dem ligamentum spirale, die sich wie bei den Vögeln und Crocodilen am oberen Schneckenende vereinigen."

"In der Lichtung desselben gegen die scala tympani, also nach innen gewandt, spannt sich die vom Anfange der Schnecke bis zum Ende derselben, dem Kuppelblindsacke, allmählig und gleichmässig an Breite zunehmende membrana basilaris, wäh-

rend nach aussen, zwischen den äusseren Theilen des Nerven- und dreieckigen Knorpels, dem limbus cartilagineus und dem ligamentum spirale, an der scala vestibuli sich die nicht länger quergefaltete, sondern in der ganzen Ausdehnung glatte, zarte membrana Reissneri ausspannt."

"Was nun die macula acustica des Schneckenrohres, des organon Corti der Autoren, betrifft, so finden wir dass dieselbe nicht wie bei den übrigen höheren Wirbelthieren, von den Schlangen angefangen, theilweise auf der membrana basilaris, theilweise auf dem Nervenknorpel, dem limbus spiralis cartilagineus ruht sondern wir sehen, dass sie den grössten Theil der membrana basilaris, vom Ansatze an den Nervenknorpel angefangen, einnimmt und das ist ein interessantes Verhalten, da wir wissen, dass von den Schlangen bis zu den Vögeln ein immer grösserer Theil der Basilar-membran die Nervenendapparate trägt, die sich nun nicht bis in den Grund des Kuppelblindsackes, der lagena, wie bei den übrigen Vertebraten, sondern nur bis an die Grenze desselben erstreckt, so dass also die lagena der Säuger und der Menschen im Gegensatze zu der der ubrigen Wirbelthiere nicht von Zweigen des acusticus versorgt wird."

The evidence of comparative anatomy leaves no doubt of the direct descent of the mammalian cochlea from the reptilian type. The relationship of the birds to the reptilia needs further investigation before any satisfactory conclusions can be reached. But I think that we are no longer entitled to place the birds next the mammals and higher than the saurian reptiles in respect to the degree of development of their auditory organs.

Although *ontogenetic* evidence seems to lead to the conclusion that the auditory organ arose by the invagination of *a single superficial sense organ*, it is by no means certain that this is true; for there are certain facts of comparative anatomy and certain phylogenetic considerations which point to the conclusion that the auditory organ has arisen by the bringing together of two originally distinct sense organs which were together sunk below the surface. The main facts at present in favor of this view are these: —

1. In all eared vertebrates the auditory organ is supplied from two distinct brain centres (*i e.* the ear nerves run from

the cells of origin in the ear to the so-called nuclei in the brain), one lying in close connection with the facial nuclei, the other intimately related with the glossopharyngeal nucleus.

2. In all eared vertebrates the so-called auditory nerve is composed of two distinct roots — an anterior and a posterior — which supply the anterior and posterior chambers respectively.

3. In all these forms the anterior root is external to the brain, united with the facial nerve.

4. In some fishes the nerve to the posterior ampulla is derived from the glossopharyngeal nerve, between which nerve and the posterior root of the auditory there exists, however, a more proximal connection.

5. The auditory vesicle is always developed between the facial and glossopharyngeal nerve roots.

6. The endolymphatic ducts are supplied on their mesial faces by branches of the utricular and saccular nerves, while the distal end of the saccular duct, in some fishes, opens into a canal containing sense organs innervated by the glossopharyngeal nerve.

7. The so-called eighth cranial or the auditory nerve must have arisen from branches of two distinct cranial nerves, and is not homodynamous with such cranial nerves as the fifth or tenth, as we now understand them. This is true (*a*) because the auditory sense organs thus supplied were primarily only a portion of the canal sense organs innervated by the original nerves of the pre-auditory condition of these sense organs; (*b*) because the auditory nerve is clearly not a complete nerve, and is not even equivalent to a dorsal root of a cranial nerve, for its two divisions are probably merely branches of the dorsal roots of the seventh and ninth nerves, since they draw off only a portion of the sensory fibres from these two nerves.

The primitive division of the auditory chamber and its nerve supply into two so sharply marked portions is thus phylogenetically accounted for, and at the same time the early ontogenetic changes in the auditory vesicle receive their explanation.

The two sense organs, the maculæ acusticæ of the utriculus and sacculus, are thus derived from two organs terminating two separate canal systems which had, as they may still be seen in Amia, become confluent on the surface of the body midway between the roots of the facial and glossopharyngeal nerves as

they issue from the brain. At the point of junction the two half-pores united into a single pore, which in some fish forms (*e.g.* Torpedo) persists as the outer opening of the endolymphatic duct, and the only persisting indications of the separate origin of these organs and their canals is their nerve supply. It is a necessary consequence of the great functional differentiation which the ear organs have suffered that their nerves should also become much increased in size, and instead of appearing now as *nerve branches* they have become really larger than the parent nerves from which they arose. (Cuts 1 and 25, Pl. I, Figs. 1, 15, and 16, and Pl. IX, Figs. 2, 3, and 4.)

The vertebrate and invertebrate auditory organs, although parallel and analogous developments, are in no sense homologous structures, notwithstanding the apparent homology of the embryonic organs at one stage of their development in vertebrates with those of the invertebrates.

The only attempt to utilize the facts of embryology to obtain a solution of the phylogenetic questions of the vertebrate semicircular canals is that made by von Noorden, and illustrates how completely he failed to comprehend the significance of the transformation processes within the ear of the bony fish, which he had so clearly seen and described. Our author gives a purely teleological explanation of the processes he studied, and makes no attempt to bring them into harmony with the processes of canal development, of which he was cognizant in other forms — mammals especially. In conclusion, von Noorden expressed a conviction that the study in other forms of the processes he had described for bony fishes would, to use his words, "manches neu und interresante zu Tage bringen."

I quote his explanation mainly because it is unique in the literature of the subject, and because it serves to show how far away from a comprehension of the significance of the details of auditory development even the investigators in this field have been.

"Der Weg, den die Natur einschlägt, um zum Ziele zu gelangen, ist ein ausserordentlich einfacher. Das Problem, welches sie zu lösen hatte, war: aus einer einfachen Hohlkugel einen Raum mit mehreren Abtheilungen herzustellen. Die Natur umgeht es, die einmal angelegte Wand, welche den Hohlraum von der Umgebung scheidet, in ihrer Form zu

ändern, Rinnen in derselben anzulegen, die später zu Röhren abgeschnürt werden. Ein solches Unternehmen wäre vergleichbar dem Beginnen eines Baumeisters, der einen Raum auf allen Seiten mit Wänden umgiebt und nachher einen Theil der Wände wieder einreisst, um dadurch eine Verbindung jenes Raumes mit ringsumher befindlichen Räumen herzustellen. In vielen Fällen verfährt die Natur in solcher Weise. Wie viel einfacher gelangt sie hier zum Ziel! Zunächst stellt sie die äusseren Wande des gesammten Raumes, dessen sie bedarf, her. Dann treibt sie spitzenförmige Auswüchse von der Blasenwand in das innere, die zu Balken sich vereinend, sich wie Lehnen in einer Hohlkugel verhalten und von vorn herein durch ihre Richtung die Richtung der Bogengänge bestimmen. Das Material, auf welchem sie diese herstellt, ist das einfachste, welches im thierischen Körper vorkommt. Es scheint der Natur zunächst nur darauf anzukommen, in möglichster Eile ein Model zu schaffen, welches sie später durch vollkommeneres Baumaterial ersetzt. Der morphologische und histologische Entwicklungsprocess, den ich für das Gehöhrorgan der Knochenfische beschrieb, ist so eigenthümlicher Art, das man mit Recht fragen kann ob ähnliche Vorgänge nicht, auch bei der Entwickelung des Gehöhrs der Amphibien, Vögel und Säugethiere sich abspielen. Es wäre sehr wunderbar, wenn eine derartige originelle Entwickelungsart nur auf die Fische beschränkt wäre."

After bringing together the results of the many years of work on the vertebrate ear which he and other students working under his direction had obtained, Carl Hasse tells us that having carried out his plan of studying the morphology of the ear through the whole vertebrate series, he will attempt to solve the problems of the phylogeny of the vertebrate ear. The axiom governing the ideas which he puts forth in this connection is that of the continuity of the animal series. He formulated a ground plan of the animal auditory organ on the basis of the invertebrate organs, more especially those of the Mollusca. But to go still further back, he says (*loc. cit.* p. 5): "Als einfachste Form des Gehörorgans wäre wohl eine an der Körper oberfläche befindliche, mit einem oder mehreren cuticularen, starren, nur durch Schallwellen ewegbaren, frei in das den Körper umgebende Medium ragenden Härchen versehene Zelle

zu denken, an deren centrales Ende eine von einer Ganglienzelle ausgehende Nervenfaser träte, die dann Entweder wie mir am wahrscheinlichsten durch das Innere der Zelle, oder über die oberfläche derselben bis an die Basis des Haares oder der Härchen, vielleicht unter Theilung verliefe und hier mit einem leicht veränderlichen Körperchen ende." With this as a basis he passes on to a survey of the auditory organs of the main divisions of the animal kingdom. It is unnecessary to follow further in this direction, for it is not possible at the present time — much less so than when Hasse wrote — to homologize the various so-called auditory organs of the invertebrates even among themselves, and as the evidence accumulates we are carried further and further away from the conception of a genetic relationship of the vertebrate to the invertebrate auditory organs of any group. Hasse's basis for the origin of the auditory organs of all animals, — *i.e.* the hair-bearing nerve-end cell is doubtless true, — but the same may be said of all sense organs, and it is most probable now that the auditory function as such was not assumed or acquired until after such sensory cells became aggregated into groups or sense organs proper.

I think that the views here briefly outlined, while certainly not to be considered final or as all of them completely demonstrated, may, nevertheless, serve to point out to us the salient features of the future mammalian ear, since they are not without an extensive morphological foundation.

From the beginning the vertebrate auditory organ as a single one (or a pair of) canal organs through modifications which it (they) have suffered in the descent of the phylum, the canal organ has been gradually losing ground and has been more and more replaced by modified descendants, the most complicated and peculiarly modified of which is the chain of transformed organs known as the organ of Corti among the Mammalia, which has descended from the papilla basilaris of the lower vertebrate forms.

The organ thus modified is typical, I think, of the future ear, which will not retain much else than the cochlea. The semicircular canals will disappear, the maculæ sacculi and utriculi will gradually atrophy and their chambers become much modified or entirely aborted.

The typical mode of disappearance of these organs is, I think,

foreshadowed in the disappearance of the crista abortiva and the papilla lagenæ, both of which "disappear" by failing to appear in the development of the ear of those forms lacking them, and they consequently are to be counted in as members of the organ complexes forming these so-called auditory maculæ. Now extending this process further, guided by abundant indications found in the mammalian ear, we find the cristæ acusticæ anterioris and horizontalis failing to bud off from the macula acustica utriculi and the crista acustica posterioris remaining in the macula acustica sacculi along with its abortive sister organ. Thus the sense organs of the ear located in the parts first developed in point of time and present in even the lowest forms above the Cyclostomes are reduced to the Cyclostome type, and unless some new need of the organism calls upon the declining maculæ and revivifies them, we may expect them to become more and more undeveloped, until finally the cochlear organ alone will seem to be a product of the auditory involution as represented in the adult anatomy, while for a time the rudiment of the canals and later of the sacculus and utriculus in something of their pristine independence will appear as ontogenetic structures whose significance will hardly be understood if our literature shall have failed our descendants. That this condition of things is in the remote future goes without saying, but that in essentials the above picture is trustworthy cannot be doubted by those who believe in the law of evolution and the manifestations of its workings presented to us in the story of the origin of the vertebrate ear and its manifold transformations down to the present time.

As regards the modifications of the accessory acoustic apparatus, I have nothing to add to the little already given. I have paid but slight attention to its history, mainly because it is not essential to the acoustic function and also because it lies beyond the limits of, and in no way influences the conclusions of this study.

F. Physiological.

Eine höchst wichtige Betrachtung in der Geschichte der Wissenschaft ist die, dass sich aus den ersten Anfängen einer Entdeckung Manches in den Gang des Wissens heran und durchzieht, welches den Fortschritt hindert, sogar öfters lähmt. So hat auch jeder Weg, durch den wir zu einer neuen Entdeckung gelangen, Einfluss auf Ansicht und Theorie. Was würden wir von einem Architecten sagen, der durch eine Seitenthüre in einen Palast gekommen wäre, und nun, bei Beschreibung und Darstellung eines solchen Gebäudes, Alles auf diese erste untergeordnete Seite beziehen wollte?

Und doch geschiet dies in den Wissenschaft jeden Tag.— Goethe.

1. Introduction.
2. The equilibration and other theories of the function of the semicircular canals.
3. Theories of audition.
4. The canal organ theory of the function of the auditory sense organs of existing vertebrates: physical, physiological, and psychical acoustics.

In reconsidering the functions of the vertebrate ear from the canal-organ standpoint, a new theory of audition will be developed in harmony, not only with my discoveries in the anatomy of the ear, but also with the generally accepted ideas of the processes involved in sense perception by hair-bearing sensory cells. I believe, however, that we have very slender foundation for forming final judgments of the functional relations of any parts of the internal ear, and that at present what we imperatively need is not speculation, but *experimentation*. Careful, extended, and unbiassed experiments on the sense organs of the lateral line system of the lower vertebrates, to determine what is their function and how it is carried out, and then more experiments on the ear of the less differentiated representatives of our type, to determine what functional changes have arisen during the transformation process, and then finally the combination of the knowledge thus gained with the results of experiments upon the human subject. If proof is demanded for the statement that most of the speculation and experimentation on the auditory function, especially as regards its different phases, has led for the most part to ephemeral results, it is easily forthcoming, for there are few investigators who during the last half-century have written on this subject but regret the paucity of facts and the evident insufficiency of the prevailing theories.

In Hermann's *Handbuch der Physiologie*, III, 1879, p. 138, Hensen, in writing on the auditory function, says: "Trotz ausgiebigen Studiums der Literatur und trotz eigener, seit 10 Jahren gemachter Erfahrungen kann ich für eine Schlussfolgerung genügende Basis nicht gewinnen." Although this was written in connection with his essay on the functions of the semicircular canals, I think it would need very slight, if any, modification in order to extend it to all other parts of the auditory canal complex and the contained sense organs. As Hasse had found the *lack* of a sufficient basis for generalization the one characteristic common to all the works on the morphology of the ear, so Hensen has found a similar lack of a basis of facts sufficient for satisfactory conclusions the ever-present character of the literature of the physiology of the ear.

Under the circumstances one is hardly to be pardoned for writing more words on the subject unless he shall add to a foundation of fact, and not merely to one of speculation.

Most physiological laboratories contain an ever-increasing quantity of apparatus and experimental devices which, having served their purpose, are laid aside. They have, perhaps, been instrumental in making important advances in knowledge, but are now no longer useful, owing to, it may be, the very advances they themselves have been instrumental in bringing about. As a rule, however, so far as any future advance in the physiological domain is concerned, this apparatus is useless. It may have an historical value, it is true, and is often preserved for this reason alone.

I think it cannot be gainsaid that all of the theories with reference to the physiology of audition are so entirely inadequate that to continue their use is to hinder the progress of knowledge. Hence these theories stand in the same relation to the literature of this subject that the antiquated apparatus does to the newer investigations of the laboratory. If what has been written about audition is in the main inoperative, the only promising way to the light is a return to first principles. We must experiment for facts and relations on which to build up a consistent theory.

If our predecessors had only begun with the alpha, and learned the auditory alphabet morphologically as it is displayed in nature, instead of learning the form of the omega of the

series alone, and endeavoring from their very imperfect knowledge of its morphological relations to understand its physiological laws, we would, doubtless, be much nearer than we are today to an adequate understanding of human audition. More than four centuries before Christ, Empedocles is said to have referred the auditory impressions to the cochlea. In our year, A.D. 1891, we are not able to do much more, notwithstanding our accumulations of anatomical details.

About all we know of audition is: 1st, That the ear is the auditory organ; 2d, That the sensory hair cells (auditory nerve origin cells) of the ear are in some way instrumental in transforming wave motions into auditory sensations.

The amount of experimental knowledge of the functions of the lateral line organs is very limited indeed. Wiedersheim summarizes the contributions to the subject in the following words (*loc. cit.* p. 363): "Was nun die *Wirkungsweise* der Nervenhügel und ihre verschiedenen Modificationen bei Fischen und Amphibien anbelangt so kann ich füglich absehen von einer Erörterung der von den verschiedensten Seiten darüber aufgestellten Hypothesen. Mit voller Sicherheit lässt sich darüber nichts behaupten, die grösste Wahrscheinlichkeit hat jedoch die von Merkel aufgestellte Ansicht, nach welcher es sich keinesfalls um einen *chemischen*, sondern nur um einen *mechanischen Reiz* (Erschütterung des umgebenden Wassers?) handeln kann." "Wir hätten also Tastorgane vor uns. . . ." Mayser and Emery consider the organs of the lateral line system to form an accessory organ of hearing, whose function, even if not strictly that of the perception of sound wave motion, nevertheless comes within the territory of the auditory function.

Mayser found that the central terminations of the nerves originating in these organs were intimately related to the auditory centre in the medulla, and based his conclusions as to their function mainly on this anatomical connection.

We are thus enabled to understand how the organs of the lateral line system, especially those in the head region, must have a function analogous, if not identical, with that of the auditory sense organs; for they both take up vibrations from a circumnatant liquid medium and transmit them to the nerve ends, and both have, likewise, the same origin ontogenetically.

While one set of organs has retained its *primitive* adult

relations, even in the adult forms of the present day, the other has been modified so as to form the internal ear in the manner already described.

The lateral line organs take up their wave motions from a more limpid fluid than the ear organs, since the endolymph contains a quantity of mucin and earthy matter in solution, which not only increases its specific gravity, but gives it a certain viscidity. This denser medium of the internal ear is more favorable to the rapid transmission of auditory stimuli than water, and it may be that in this fact we have an explanation of the origin of the mucous canals of Elasmobranchs.

The lateral line organs also perform an important function indirectly as *organs of equilibration*, since they convey to the centres of co-ordination information of the direction in which matter in space surrounding the animal is moving.

Suppose a fish to have its body rotated about the long axis; it is evident that this motion will cause two currents to be produced, setting in opposite directions. Thus, if the rotation is from the right to the left, or with the hands of the watch, the current on the left side will be upward and the current on the right side will be downward, when judged from the fish's standpoint; for though the water moves not at all, the fish would refer the movement to the water, since the sensation of motion would be taken up from or caused by the water.

These organs are also auditory in a sense; for they are like the special auditory organs in their structure and central nerve relations, and since the ear organs have been derived from, and what is more important still, since at least three of the sense organs of the auditory apparatus retain all the characteristics of the superficial organs, we may reverse the line of argument, and say that all the external organs are primarily auditory in function though in an undifferentiated degree.

After a brief resumé of the main historical features of the semicircular canal question, we will pass to a consideration of the function of these famous tubes and their inclosed sense organs, the cristæ acusticæ, in the light of new facts brought forward by a series of experiments recently carried out by Professor Steiner of Heidelberg University, and of the new morphological considerations already given in this paper.

The semicircular canals have been the subject of untold num-

bers of experiments, and hundreds of vertebrates, high and low, have lost their lives on the altar of science (the protests of the anti-vivisectionists notwithstanding), without the attainment of the results hoped for, since the object of this sacrifice — the determination of the *function* of the semicircular canals — had become more and more difficult with the increase of physiological experiments.

This result was mainly due to the firm belief which had become the basis of most attempts to solve the questions relating to the ear canals; viz. that the canals must have some function of a peculiar and special nature, which, owing to their spatial relations, must be closely connected with the equilibration of the body. This view was supported by the fact that with two exceptions all species of vertebrates had the same sort of apparatus. The ear as a whole was treated as something unique in the animal body, with no genetic relations to other structures, and the canals, highly specialized portions of the ear organs. It was perhaps impossible to make much progress so long as this belief was allowed to dominate all conclusions from speculation or experiment, but more might have been done had physiologists earlier taken hold of the sadly neglected field — comparative physiology.

The first experimentalist to take up the subject of the function of the semicircular canals seems to have been Flourens, who in 1828 found that Pigeons with resected semicircular canals were unable to control the movements of their heads, and his observations were later repeated by Cyon (62, 63, 64), who described the phenomena attending the division of the canals as follows. After section of the external semicircular canal the Pigeon moves its head from side to side around an axis passing vertically through the head as the bird stands.

After section of the posterior canal the movements are up and down around a horizontal axis passing through both ears, but after section of the anterior semicircular canal the movements are diagonal components of the two just described. These pendular movements cease after a time when the section is one-sided, but they are more intense and persist longer when they are bilateral.

Flourens and Cyon maintained that the movements always occurred around an axis at right angles to the plane of the sec-

tioned canal. Although hearing did not appear to be destroyed, the locomotion of the birds was seriously impaired, and not infrequently indications of muscular paralysis made their appearance. To Flourens the explanation, that these disturbances were due to injury to the fibres of the nerve of hearing, was not satisfactory, and he was led to the view that the cochlear nerve was composed of two sorts of nerve fibres. One set composing the cochlear nerve subserves the function of audition, while the other set composing the vestibular nerve subserves the equilibrious function and is distributed to the semicircular canals. Injury to the former produced deafness, while injury to, or destruction of, the latter was followed by the phenomena described above. Similar results with more details were obtained on repetition of these experiments and with some variations of the conditions by Czermak, Harless, Brown-Sequard, and Vulpian; and although it was generally agreed that injury to the semicircular canals of birds and mammals (the animals mostly experimented on were Pigeons and Rabbits) or the vestibular nerve was followed by disturbances resembling very closely those following operations on the cerebellum; and although Flourens had advanced the view that the vestibular nerve was the peripheral extension of the cerebellar peduncles, these later observers did not agree with Flourens that the disturbances following *operations* for canal section were due solely, or in great degree, *to the section of the canals.* Brown-Sequard explained the phenomena by assuming the existence of special sensory fibres in the vestibular nerve which by reflexes caused the muscular contractions producing the motor disturbances.

Vulpian, on the other hand, sought the cause of the trouble in an "auditory tumult," caused by continued abnormal stimulation or irritation of the auditory nerves.

Loewenberg (1872, 186) experimented with Pigeons after removing their forebrains, and concluded that section of the semicircular canals produced the motor disturbances by irritating the membranous canals, not by laming their sense organs; and the disturbances were entirely reflex without the least participation of consciousness.

Up to this time the subject had not been advanced beyond the condition in which Flourens had left it; but in 1870 Goltz gave a new aspect to the problem by explaining the observed

phenomena in the following manner. This author recognizing the great similarity between the motor disturbances in Pigeons whose heads are fixed in abnormal positions and those whose semicircular canals have been cut, concluded that since when the canals are injured the animal loses control of its head (and body), and since when it is forced to lose control of its head with canals intact it likewise loses control of its body, it was evident that the semicircular canals form an apparatus subserving the equilibrious function, and the cristæ acusticæ were in reality the equilibrious sense organs of the head and mediately of the body entire.

Goltz assumed that the sense organs in the ampullæ were capable of being stimulated by pressure or other mechanical change similar to the nerves of the skin. The stimulation necessary for perception of spatial relations was supplied by the column of endolymph contained in the canal. Since this fluid would press most strongly on the lower parts of the canals, and since with variation in the position of the head one or other of the three canals would serve as vertical canal or horizontal canal, Goltz thought to have discovered the modus operandi of the canal function.

Each position of the head would be represented by a specific nerve stimulation from which the animal would be able to judge of its position in space. If, however, the canals were injured, these nerve stimuli, on which the animal depends for regulating its body, are due to injury, and consequently convey false information; the co-ordinating apparatus making use of these stimuli induces false movements, or, as we say, co-ordination of movement is destroyed, and equilibrium of the body is lost. In 1872, Cyon re-examined Goltz's hypothesis and formulated a theory embodying the same ideas, and the same view was accepted on experimental evidence by Mach (1875, 188[b]), Breuer (1875, 41), Crum Brown (1874, 43[b]), Spamer, and some few others. About the only difference of views between these later observers and Goltz is the assumption by the former that in the movements of the head currents are set up in the canals whose flow will depend upon the amount and rate of the motions of the head. Thus they sought to establish the so-called dynamical theory of the semicircular canals as expressing more of the truth than Goltz's statical theory. This latter theory could only

be maintained by assuming that the motions of the head and sensations of giddiness on canal section were due entirely to the injury inflicted on the canals, and Goltz recognized three essential structures, the injury to any one of which would be sufficient to cause the disturbances observed on what was supposed to be simple canal sections: the central organ, the peripheral end organs and their connecting fibres with the central apparatus, and the motor apparatus and connections. If, then, the disturbances were due solely to the section of the canals, it must be true that no injury to the brain has taken place. Goltz believed that injury to the brain was rigorously excluded in his operations on the canals.

Goltz, Brown-Sequard, and Flourens all agree that there must be other nervous elements present in the auditory nerve besides those ordinarily recognized and to whose irritation the phenomena of giddiness were due, an assumption which the investigations of Magendie, Valentine, and Schiff contradict. Schiff (1859, 252) says: "Die Hypothese, dass der Acusticus in zwei Nerven zerfalle, von denen der eine dem Gehör diene, während der andere die eigenthümlichen Bewegungen des Kopfes vermittle, die Flourens nach der Durchschneidung der halbzirkelförmigen Kanäle beschrieb, entbehrt aller Begrundung."

Let us examine how far Goltz's view has been sustained. Pathologists believed that the evidence from pathology was not in favor of Goltz's view, and Boettcher by careful experimental investigations on Pigeons proved that Goltz's hypothesis rested on false conclusions drawn from incomplete knowledge of the results of the so-called canal section. It is not true that motor disturbances of the body are direct consequences of the abnormal position of the head following canal section, but, on the other hand, the abnormal position of the head is a consequence of injury to the brain as a result of the operation of canal section as carried out by Goltz. Boettcher concluded that all disturbances of the motor apparatus after canal section were referable to brain lesions, especially to the cerebellar peduncles, since he was able to section the canals without the appearance of the motions attributed to them.

Boettcher's observations were thoroughly substantiated by the experiments of Fraulein Tomaszewicz (1877, 276). As Boettcher had already resected the horizontal and vertical canals in

the Frog without producing the least disturbance of equilibrium, so Tomaszewicz was able in her experiments on bony fishes to remove the semicircular canals without the fish showing the slightest traces of a disturbance of equilibrative power. These results agree entirely with those obtained by Kiesselbach in his successful operations. Finally, Cyon demonstrated that these motions and equilibrious conditions could not be due to the *functions* of the canals, *since the same phenomena occurred after section of the auditory nerve*, and that rotation of a mammal in this condition brought on vertigo the same as in entire animals, completely exploding the dynamical theory.

Notwithstanding these investigations, Helmholtz (1877, 120), in the last edition of his *Tonempfindungen*, p. 249, practically adopts Goltz's view. Older experiments by Valentin and Schiff, in which these investigators had been successful in cutting the canals without bringing on motor disturbances, remained unnoticed while the work of Flourens, Brown-Sequard, Breuer, Mach, and Crum Brown, who had not succeeded in cutting the nerves or canals without such disturbances appearing, were given more weight than was their due. Cyon's experiments in 1878 on Petromyzon were always followed by motor disturbances, but such a result was to have been expected, owing to the compactness of the parts and the practical impossibility of isolating the canals in such an operation.

The following observations, cited by Baginski, to whose account I am indebted for these important facts, were made by H. Munk on a Dog which had for several months suffered with dizziness and malposition of the head. Examination showed that the trouble was caused by a distension of the tympanic cavity with a liquid exudation. This fluid had not entered the canal complex, and apparently had *not* caused lesion of the latter nor of the brain. Here was a case showing symptoms similar in all respects to those following the experiments of Flourens and Cyon on resection of canals in mammals.

A solution of the ear canal problem might be possible if the relation of the ear canals in this case to the abnormal symptoms could be determined, but this could not be done owing to the *impossibility* of operating upon the canals in mammals without at the same time injuring the cerebellum, owing to its closeness to the ear and the very intimate relation of both structures to

the bony wall separating them. Search was made for some means of arriving at the same goal experimentally. This pathological condition suggested trying if increase of pressure in the tympanic cavity would not produce the same symptoms as had been observed in the two sets of cases detailed above. Salt water of three-fourths per cent strength and varying in temperature from 9° to 15° C. was injected into the tympanic cavity and produced with increase of pressure malposition of the head and nystagmus.

These symptoms continued to increase in intensity with the increase in pressure. Most of the animals thus operated upon recovered after unilateral injection; the majority of those subjected to bilateral injection usually died after a few days from what the symptoms and post mortems proved to be inflammation of the brain. With water at 38° C. the pressure required to produce these symptoms was greater than when colder water was used, and most of the bilaterally injected animals lived, only a few dying of inflammation of the brain. Other fluids were used, *e.g.* concentrated salt solution, ammonia solutions, etc., and they all produced the same symptoms, with rolling movements. In these experiments the symptoms were the more intense, the greater the chemical activity, and the greater the pressure or the more rapid the injection. The death of the animal operated upon usually followed in these cases on the same or the following day, and post portem examination usually showed hyperæmia or œdema of the brain, with inflammation or hemorrhages of the parts of the brain subjacent to the ear. These observations did not allow of any other interpretation than that the fluids had penetrated to the brain, and the careful examination showed that the membrana fenestræ rotunda was always ruptured, allowing penetration of the liquids from this foramen through the perilymphatic spaces into the subdural space, and from here on to the brain. As I have already shown, the endolymphatic and perilymphatic spaces both communicate with the cranial cavity, but in Munk's experiments the communication was largely increased by rupture. Hydrostatic pressure obtained by introducing a glass tube into the tympanic cavity and filling it with water induced the same symptoms; but if the symptoms did not make their appearance after a certain pressure was reached, they remained permanently absent. Wherever the

symptoms appeared the membrane of the round window was found ruptured and the liquid found in the subdural space, about the brain, and especially abundant at the mouth of the aquæductus cochleæ in the jugular fossa. These results are in harmony with those obtained by Brown-Sequard, Magendie, Schiff, and Schwan, who, by direct mechanical stimulation of that portion of the corpus restiforme lying on the fossa jugularis, had previously produced similar motor disturbances. Giddiness is then a result of irritation of the brain, complicated in these experiments with an irritation of the ear channels. In order to obtain a more precise answer to the problem, it was necessary to find a method of irritating the ear channels alone with the complete protection of the brain. By an easy operation on the Dog, following Haidenhain's method, the position of the internal ear may be exposed for operation by a removal of a piece of the ventral wall of the tympanic bulla. According as this operation is carried out, uni- or bi-laterally, is the animal made deaf in one or both ears. The animals thus operated on never show any trace of motor disturbances or of loss of the power of equilibrium.

If such an animal is killed some months after the operation, the entire internal ear is found in an advanced state of fatty degeneration. The sacculus and utriculus are frequently not recognizable, while the cochlea is transformed into a cicatricial tissue. If instead of destroying with the instrument only the utriculo-sacculus and the canals, the cochlea as well is broken up or removed, nystagmus and malposition of the head are the immediate symptoms, and they are accompanied by deafness. Post mortems of such cases always showed that in removing the cochlea the porus acusticus internus was exposed or injured, and by the rupture of the auditory nerve the cranial cavity was opened; consequently in this operation the cerebro-spinal fluid must always escape. That in rupturing the auditory nerve the brain tissue is injured is quite apparent. Whereas such lesions are always followed by dizziness and equilibrative disturbances, such disturbances do not appear when the cochlea is preserved, and only the utriculo-saccular and canal end organs are destroyed and resorbed by the healing of the wounds. Giddiness does not result from the destruction of the auditory organs, but only from lesions of the brain; and since the semicircular canals can

thus be destroyed even in mammals without producing equilibrative disturbances, there is no question that the disturbances seen to follow canal section in Pigeons are not due simply to the section of the canals.

The disturbances appearing after canal section are of two kinds, — those appearing immediately after the operation and those which make their appearance some time (usually several days) after the operation, *e.g.* malposition of the head, on which Goltz laid so much stress. Pigeons thus operated on and showing the characteristic disturbances, when studied (dissected) five to eight days later, showed conditions similar to those just described for dogs. The injured ear was found to present a bony scar, within which the semicircular canals were hardly discernible. The larger ear chambers were entirely degenerated and converted into pus, and the inflammatory process had affected the brain, especially the vermis, which was usually found degenerate. While in such cases the abnormal symptoms only appear slowly as the cerebellar inflammation progresses, they may be brought on suddenly by deeper lesions; and in all such cases blood was found in the medulla near the entrance to the fourth ventricle, and small hemorrhages were found in the cerebellum and pons. Since injury to the vermis is followed by malposition of the head, we must conclude that the inflammation and hemorrhages in the same parts cause the motor disturbances, and that these are due always to an affection of the brain, which either appears immediately after canal section or else later, induced by the inflammatory processes. Goltz's ideas are thus proven to be incorrect and his deductions refuted.

Baginski was never able to confirm the results obtained by Flourens, Goltz, Cyon, according to which there existed a constant relation of the motions of the head to the plane of the canal (or canals) cut. He found, on the contrary, no constancy in the symptoms after the same operation on different animals, and he concludes that after careful and exact observation he is certain that the assumed relation between the position of the semicircular canals and equilibrative disturbances following their section does not exist. The co-ordination disturbances of the body are not in any way subject to the spatial relations of the canals. The falling and pitching movements occurred in

the same direction indifferently, whether the horizontal or vertical canals were cut.

Although there is a certain dependence of the disturbance on the direction of the canal sectioned in the pendular movements of the head on section of two canals, there are frequent enough undeniable variations. It is especially to be noted that the pendular motions of the head may be entirely absent, as happens most frequently, and at the same time often, in section of the posterior canal, and they may be replaced by others: the malposition of the head is such as usually only occurs after several days. Hensen has likewise pointed out that when motion follows canal section it is apparently due to the current of escaping lymph flowing on through the ear, which of course would cause irritation of the sense organ belonging to the canal, and thus give rise to the sensation of pain, the feeling of being wounded, which is also sufficient to account for all the motions observed. When one remembers in this connection that the malposition of the head may persist for a month or two and then give way to a return of the pendular motions, it is apparent that the latter have their cause also in the central disturbances. This deduction finds weighty substantiation in the configuration of the parts and in the very intimate connection between the brain and the semicircular canals. In Pigeons, the *aquæductus vestibuli*, after passing through the apertura aquæductus vestibuli, according to the investigations of Hasse and Boettcher, opens into the subdural space. Consequently the endolymphatic fluid is continuous with the cerebro-spinal liquid, as Schwalbe and F. E. Weber have proven. In each operation of canal section there is thus brought about a change within the cranial cavity which has direct influence on the brain. Since the cranial cavity is opened on canal section, the pressure conditions of the brain are at once altered, owing to the escape of endolymphatic fluid and cerebro-spinal liquid. The pressure is of course suddenly lowered, and Magendie has shown that the usual consequences of tapping these liquids is the so-called "Taumelerscheinungen."

Thus the primary symptoms are explained, which, so far as motor disturbances of the body are concerned, are only different in degree, as one or both sides are operated upon. The pendular motions of the head are more difficult of explanation, following

the sections of two like canals of two sides of the head, since a certain relation of the direction of the pendular motions to the canals cut had been noticed. Although the evidence thus gathered together is still insufficient to explain wholly the phenomena under consideration, it nevertheless points unmistakably to the *central* origin of these disturbances. All the phenomena following canal section in mammals and in birds are nothing more than the results of brain lesions such as are entirely adequate to explain the phenomena.

Baginski concludes from his own observations that "Sovielsteht indess fest, dass die meisten vorliegenden Untersuchungen für die Behauptung, dass die Bogengänge die peripheren Organe des Gleichgewichtunns sind, dessen Centrum in Kleinhirn sich befindet, den Beweis nicht nur *nicht* erbracht haben, sondern dass im Gegentheil dieselben ganz und gar gegen diese Annahme sprechen"; and further that "Wir wissen, ja über die Funktion der Bogengänge trotzt aller bisherigen Untersuchungen überhaupt nichts."

Retzius had already called attention to Breschet's discovery that the auditory nerve was divided into two branches, each of which supplied semicircular canal organs. But the canal experimentalists have very generally been ignorant of this important fact, and Baginski (1883, 12) introduces it for the first time into this discussion.

Steiner's (270, 1886) experiments were at first, as he himself has shown, of a nature not likely to give unmixed results, and both in operation and in result were very much like Sewall's.

However, by improvements in the surgical operations necessary to effect the separation of the canals without disturbance to other branches of the auditory nerve than those ending in the ampullæ, the experiments were finally made completely demonstrative.

Steiner was thus able to remove all six semicircular canals from the ears of the Sharks operated upon without causing the least apparent disturbance to the motor apparatus of these fishes. This experiment he repeated many times with the uniform result of seeing the fish, when replaced in water, swim off as though anatomically perfect. In this conclusive way is the question settled, — the question of the part played by the semicircular ear canals in the function of equilibrating the body; and it is

clearly shown that these canals have no *special* or *controlling* influence on the spatial relations of the body.

It is manifestly important to determine what Sewall's and Steiner's first results were due to, and Steiner carried on experiments in the endeavor to answer the question. He observed that in any Shark operated upon, whether the semicircular canals were removed or not, when the instrument disturbed the calcareous crystals covering the utricular sense organ, the animal immediately executed reflex motions or "Rollbewegungen," and as a rule the fish rolls toward the side thus disturbed.

When, however, both ears are thus injured, although the "Rollbewegungen" set in, they are too complex to be analyzed.

This investigator experimented with the utriculus by filling the whole auditory cavity with melted paraffine of low melting-point, and he found that such a procedure caused no disturbance of equilibration. He concludes from this that, contrary to what might have been expected, after the experiments on the otolithic mass of the utricular sense organ, where rolling motions followed each injury, that the function of equilibration resides not in the ear in any part. As it was advisable, if possible, to determine what causes produced the disturbance following displacement of the utricular otoliths and possibly injury to the nerve end cells of the utricular sense organ, Steiner carried on experiments to that end, and found that the disturbance in the motor mechanism is due to slight but certain and potent injury of the acustico-facial nucleus in the medulla. The injury produces motions that are not to be distinguished from those produced by section in this region of the medulla. Steiner concludes that, everything considered, we do not need a special explanation to account for the fact that careful cutting of the ampullar nerves or any injury to the ampullar sense organs which does not manage to reach the central nucleus, does not call forth rolling motions.

It is evident that Steiner's results cannot be due to a difference in character between the ampullary and utriculo-saccular nerves, for each of the two branches of the auditory nerve supply ampullar sense organs and otolith-covered auditory sense organs (*e.g.* the maculæ utriculi and sacculi); and since it is injury to the latter alone which apparently causes the equilibrative disturbances and not of the nerves alone, it would seem

that we have here to deal with a disturbance of the relations of the otoliths to the sensory hairs. The otoliths when disturbed in the normal relations would cause many kinds of distortions of the sensory hairs, such as bending, crushing, or even breaking, and in this way irritate the central end cells by a stream of abnormal impulses in such manner as to cause confusion in the auditory co-ordinating apparatus, or if continued beyond the limit of reaction it would produce exhaustion of the apparatus so used and by sympathetic relations the motor disturbances. Owing to the absence of otoliths from the ampullæ these disturbances would not be kept up after the first injury had been accomplished. Be this as it may.

Steiner has shown that medullary lesions of a light nature are within certain bounds capable of producing greater disturbance than the more extensive section of half the cord. Consequently the slight injury to the medullary acustico-facial nucleus caused by the dissection of the utriculo-sacculus and the injury of the sense organs contained gave rise to no unusual or exceptional phenomena; Steiner found also that the neighborhood of the acustico-facial nucleus was the most sensitive region of the whole medulla in sharks, and I am able to confirm his conclusion from my own experiments on frogs by means of the electric current; other points on the floor and side walls vary a great deal in their relative sensitiveness.

The final conclusion is as follows: "Nehmen wir Alles zusammen, so folgt, dass die halbzirkelförmigen Canäle der Haifische so wenig wie der N. *acusticus* zu den Bewegungen resp. deren Gleichgegwicht in irgend welcher unmittelbaren Beziehung stehen, und dass die Störungen, welche Man nach mechanischem Angriff auf den Vorhof thatsächlich beobachtet, Zwangs bewegungen sind, welche ihre Ursache in einer mittelbaren Läsion des Nackenmarkes an der centralen Ursprungstelle des Hörnerven haben."

This demonstration is as definite in result as it is decisive of the canal question so far negating the assumed functions. Considering the ease with which it is performed, we can hardly understand why it had been so long postponed.

As Foster has shown, in those experiments involving the use of several *special senses*, the organs supposed to be special organs of equilibration are found to be less potent in this regard

than the eyes. If the canals were specially charged with the equilibrative control of the body, why do they not overcome the abnormal but powerful and for the time being controlling sensations induced by rotating the body with the eyes open?

It seems to me that there can be no question that all the theories and the supporting experiments have, not only *not* proved that the semicircular canals have any function whatsoever, but that they have, on the contrary, proved conclusively that providing they have a function, it is not either statically or dynamically equilibrative nor in any way connected with the spatial relations of the canals. The favorite and certainly one of the very best arguments to be brought forward as proof of the function of an organ is that the morphological relations not only favor or are entirely in harmony with the assumed physiological action of the organ, but are such as render the function ascribed the only available or the most highly probable function.

This argument from structure to function has been applied to the ear canals from the time when the theory, according them the function of determining the directions in space, was put forward by Scarpa, and the justice of the application no one has questioned, and the argument has retained its ascendency in the minds of physiologists above and beyond all negative testimony heretofore adduced.[1]

Although at present there are no more important facts to be brought out, an examination of the views of a few more anatomists will prove instructive. In the last edition of his *Text-book on Physiology*, Foster says (p. 1013): ". . . that afferent

[1] Since Scarpa's time the physiology of the ear has been furnished with the "direction" theory of the semicircular canals. Autenrieth, and later Kerner (1808), accepted and again propounded the same views, which had been generally accepted by English, French, and Italian anatomists since Scarpa's time. Johannes Müller raised objections to this view, and since his time the evidence has grown so steadily that to-day there is no longer any adequate foundation for the explanation. It has been generally discarded for many years, although several years ago Ogston again attempted to prove Scarpa's position to be the correct one. Hasse accepted no theory as applicable throughout the vertebrate series, but thought the ear might be connected indirectly with the orientation of the body. Hensen concluded that among the Mammalia, especially man, there was little probability that such a function was exercised by the canals. He attributed the perception of direction of sound to the differential action of the ears of the two sides of the head, and to the work of sensations other than the auditory. Meyer accepts this view as concerns the Sauropsida and Mammalia at least. According to Manilin (190, 1866) the semicircular canals serve to annihilate the sonorous vibrations.

impulses other than those of sight, touch, and the muscular sense do reach the brain and afford a basis of judgment as to the position of the body, does not by itself prove that those impulses come from the semicircular canals; *the arrangement of the canals is undoubtedly suggestive* [italics mine]; but it is quite possible that the afferent impulses may be generated by one or other of various changes, vaso-motor and others, of the tissues of the body which are involved in a change of position." "It cannot, therefore, be regarded as settled that the canals are the source of normal impulses, or that our conscious appreciation of the position of the head, and so of the body in space, is based on such impulses." "But such a view is not disproved; and in any case it remains true that injury to the canals does in some way or other, either by generating new impulses or by altering pre-existing ones, so modify the flow of afferent impulses into the machinery of co-ordination as to throw that machinery out of gear."

M'Kendrick (1889) on p. 701 says, after stating Cyon's position in 1872, according to which the latter investigator considered the cristæ acusticæ to be the peripheral spatial sense organs, the cristæ of each set of canals, *e.g.* the two externals, controlling a dimension of space, that "the weakness of Cyon's theory is that it offers no explanation of the mechanism of the canals."

We now come to the colophon. P. McBride, M.P., has published his views of the functions of the semicircular canals, obtained, it would seem, "durch eine Seitenthüre," if Goethe was just in asserting that science has daily to suffer from such architects. McBride's plan of the structural relations of the semicircular canals is constructed in the following manner. After showing to his satisfaction that the Cyon-Mach-Breuer-Crum Brown theory, according to which they (the canals) are the peripheral organs enabling us to estimate our position in space, is insufficient and inconsistent, he says we should admit "nothing in life is superfluous," and that "every physiological apparatus is the best possible for the well-being of the organism," and that in the animal economy "there is reason for every anatomical detail." The first of these statements is so extensive in its application as to overwhelm any but the greatest intellects, and is for the most part left undecided by experimentalists, while the second proposition is certainly not to be classed

among those questions that have been definitely decided in the affirmative either by morphologists or physiologists. As to the third thesis, our author is undoubtedly correct, but if I do him no injustice, unintentionally so; for his reasons, according to which the semicircular canals form a part of vertebrate anatomy, are not those which appear to find expression in the phylogenesis of these beautiful structures.

After stating that vertigo can only be produced by pressure on or disturbance of the ampullar nerves (an assumption which is well known to be incorrect), he says that if the canals were for equilibration only, they would probably have been put by themselves instead of being connected with the auditory apparatus, and the semicircular canals would not have been so unnecessarily exposed were this their only function, since they would thus present a striking contrast to all other physiological arrangements. "On the other hand, if they be so placed, as I believe, for some useful purpose, the most probable explanation is that while some sonorous vibrations are conveyed by the cochlear nerve to the true auditory centre, an afferent impulse is at the same time sent to the various motor centres through the ampullar nerves."

Of a truth both cochlear and ampullar nerves, as representative of the two roots of the auditory, do connect through the auditory nuclei with the motor centres, but there is no reason at present for holding that the ampullæ are *specially* connected with the motor apparatus.

Finally, to come to the main point for which this historical introduction is intended to serve as a preliminary and a preparatory, for the conclusion which I wish to draw, that the semicircular canals are so innocent of all the functions which have been heaped upon them that now that I have shown, by giving the results of the physiological experiments of other investigators, to what conclusion they have been forced to come by depriving themselves by experiment, one after another, of all the assumed facts concerning the assumed functions of the semicircular canals, it only remains for me to bring forward the architectural reasons for the semicircular canals to prove beyond doubt that they as canals have no participation in the physical processes leading up to auditory or other afferent sensory stimulations, and hence are in nowise auditory or

equilibrative in function. No part of the ear then constitutes a special organ of equilibration, of spatial sense, or of special motor control. The ear as a whole — and only because it contains sense organs, and they only because of their hair-bearing, nerve-connected cells — shares with other sense organs these important functions because of common association with motor and other centres, and has as its special function the perception of wave motion (*i.e.* changes in stress) in the circumambient water or other aqueous fluid, never of any other medium. Where the transformation of the motions thus transmitted to the auditory hairs takes place will be considered further on.

If the reader accepts this conclusion as to the function of the semicircular canals, he will certainly recognize in it an excellent illustration of the results which physiologists may hope to get from the careful study, not alone of adult structure, but of ontogenetic changes of structure. More than half a century of physiological experiment had failed to give the solution of the canal problem which the first study of their phylogenesis in connection with their comparative ontogeny at once revealed.

3. *Theories of Audition.*

It is proposed to restate in this chapter some of the problems of auditory physiology and to consider how much and in what manner they are affected by the additions to our morphological knowledge already treated of in chapter B. Hensen wrote, in 1879, "Helmholtz hat die Physiologie des Ohrs so tief und zugleich so umfassend bearbeitet, dass seine Lehren dies Gebiet mit Recht beherrschen," and one may readily satisfy himself that they *are* generally accepted by an inspection of the text-books and special papers on the subject.

Since I consider the outer and middle ear to be mere accessory structures acquired by the higher vertebrates in ever-increasing complexity for the sole purpose of enabling the animal to preserve in the aërial ocean, on or near the bottom of which they live, the necessary aquatic conditions in which they were born (phylogenetically) and which they must preserve or lose their auditory organ completely, it follows that it will be unnecessary to enter into an account of them in a discussion concerning the essentials of the auditive processes, and I may as well say at once, that according to my view of their functions, *every sense organ in the*

ear executes an auditory function, as regards essentials, in the same manner as its prototype the lateral line sense organ, and there exist between the auditory sense organs differences only in degree, not in kind, of the function subserved.

Likewise, the perilymphatic parts of the ear are not essential to the correct understanding of the auditory processes; they are simply the enlarged lymphatic spaces always developed below and around these sense organs, from the lateral line condition increasingly up to the mammalian ear.

In 1838 Duges arrived at conclusions with respect to the functions of the parts of the internal ear which were later accepted by Helmholtz. According to this view the utriculosaccular chambers subserved the functions of perceiving noises and measuring the intensities of all auditory stimuli, while the cochlea alone was capable of the perception of tone and its timbre.

Carl Hasse (1873, 118) concludes his comparative studies on the vertebrate ear with a summary of his physiological ideas in these words (*loc. cit.* p. 95): "Thus we find also in mammals and in man masses which cover the macula (Corti's organ), into which the hairs of the hair cells freely penetrate, whose innermost layer, the membrana reticularis, adheres firmly to the cells of Corti, and consequently must follow the movements of the basilar membrane.

"Should such a fibre of the membrana basilaris be thrown into vibration by the proper tone, in reptiles and birds, all of the isolation and hair cells lying on the fibre would move with it.

"They with the hairs would be moved against the membrana tectoria, whereby the stimulation of the nerve fibre which projects into the hair would be caused. The same is true of mammals and man, but in a more complete degree. The motion is propagated through modified isolation cells, attached to the fibre, which form an elastic arch, up to the auditory cells with the hairs and the membrana reticularis which are moved against the membrana tectoria.

"Thus we find that motion of the superposed groups of isolation and auditory cells is connected with the vibrations of the single fibres of the basilar membrane, while the neighboring ones do not participate, and by this means the vibration of such a cord reaches consciousness in isolation; it calls forth a special

quantitative auditory sensation, the sensation of a tone. As I indicated before, it is not thereby rendered impossible that a simple auditory sensation may arise by means of the totality of the auditory cells of the cochlea; contrariwise, this goes on concomitantly, since we know that the entire endolymph in the scala media may be set into motion through the membrana Reissneri, which then moves the entire membrana tectoria which covers all of the auditory cells and their hairs, and thus calls forth, in all, a nerve stimulation which receives no special localization characters, as in the case of the vibrations of the individual fibres of the membrana basilaris." The further details of Hasse's physiological ideas are given in the following extracts. All of Hasse's physiological ideas, which are the direct outcome of his view of the division of the ear into a pars superior and a pars inferior, are not pertinent to the present discussion, and after refuting the morphological basis on which they rested, it is unnecessary to enter into a discussion of them.

"Jede Bewegung also im cavum perilymphaticum muss sich durch die ganze scala vestibuli, an der ganzen Schneckenaussenwand, über den häutigen Kuppelblindsack (helicotrema), in die ganze scala tympani, an die gesammte Schneckeninnenwand und somit die Basilarmembran fortspflanzen, und die Zahl der Schwingungen der Knöchelchen, speciell der basis columellæ s. stapedis muss sich an der ganzen Basilarmembran und in der Endolymphe wiederholen und sich somit auch an der membrana tympani secundaria geltend machen, und das ist ja auch bis zu einem gewissen Grade unter der Voraussetzung eines bestimmten Druckes, unter dem die Perilymphe stehen muss, unter Helmholtz's Leitung von Burnett direkt bei Säugethieren und den Menschen nachgewiesen. Excessive Bewegungen werden auch hier entweder durch den ductus perilymphaticus und den peripherischen Abfluss desselben, durch das foramen rotundum, oder, wie bei den Säugern und den Menschen, durch den aquæductus cochleæ, wenn auch wegen der Enge des Abflussrohres kaum so vollkommen, wie bei den niederen Thieren, ihr Correktiv finden, ganz abgesehen von dem Muskelapparate, der sich bei Vögeln und Säugern an die Gehörknöchelchen anheftet. Die Bewegung der Gehörknöchelchen wird also eine Bewegung längs der ganzen membrana basilaris, die ja bei den Säugern und Menschen nahezu den ganzen häutigen Kuppelblindsack

absorbirt, und an der darauf befindlichen macula acustica auslösen, andererseits wird sich aber auch die Bewegung durch die membrana Reissneri, da sie auch längs dieser verläuft und diese Haut immerhin zart erscheint, am zartesten bei den Säugern und Menschen, etwas weniger bei Reptilien und Vögeln, bei denen sie möglicherweise ein Bewegungshinderniss sein kann, in der Endolymphe und somit an den Nervenendapparaten der macula und durch die Otolithenmasse der lagena der Crocodile und Vögel an den Nervenendapparaten der macula dieses Schneckentheils, in ihrer Gesammtheit geltend machen. Die letztere Bewegung, die der Endolymphe der scala cochlearis, wird demnach, da sie die Gesammtheit der Nervenendapparate wie im sacculus trifft, gegenüber der durch die membrana basilaris vermittelten, die wir später besonders betrachten wollen, eine einfache Gehörempfindung veranlassen. Keine kann sich aber in irgendwie nennenswerther Weise nach oben hin gegen den sacculus fortpflanzen, da die Communication des canalis reuniens, wie wir wissen, ausserordentlich eng und höchstens in Verbindung mit dem ductus perilymphaticus als eine Art Sicherheitsventil betrachtet werden könnte." "Somit ragen die Gehörhaare nirgends direkt in den mit Endolymphe angefüllten Binnenraum der Ampullen hinein und die Bewegung muss sich erst der membrana tectoria mittheilen. Diese wird dann auf die Gesammtheit der Gehörhaare der crista acustica, die sie deckt, wirken. Die Bewegung der Endolymphe trifft immer nahezu senkrecht auf das gewölbte, obere Ende derselben und auf die demselben aufruhende membrana tectoria und ich glaube, es wird einmal dadurch die Deckmembran auf die Gehörhaare gepresst, dann aber auch wohl ein wenig auf ihnen verschoben, und somit wird die durch die Bewegung der Endolymphe hervorgerufene Bewegung der Gehörleiste und der membrana tectoria eine Bewegung der Gehörhaare und somit den Nervenvorgang auslösen. Diese membrana tectoria zeigt bei allen Wirbelthieren übereinstimmende Verhältnisse, nur die Cyclostomen bilden in dieser Beziehung eine Ausnahme. Es ist wohl möglich oder sogar wahrscheinlich, dass dieselbe während des embryonalen Lebens auch bei ihnen als einfache Cuticularmembran existirt, allein im erwachsenen zustande erscheint sie verkalkt als eine Otolithenplatte, die sehr leicht in einzelne kugel — oder schalenförmige Elemente zerbröckelt, und wenn

ich auch nicht glaube, dass das Verhältniss derselben zum Nervenepithel und zu den Hörhaaren desselben ein anderes, als bei den übrigen Vertebraten, so bedarf dieser Punkt doch noch weiterer Untersuchungen."

In stating Helmholtz's view, let us begin with an account of what takes place when the stapes is forced into the oval window. According to his generally accepted views, when the tympanum is vibrating under the influence of aërial undulations, the stapes, owing to its mechanical connection with that membrane, executes to-and-fro movements which transfer the tympanic vibrations to the perilymph, in the form of delicate blows delivered against the surface of the fluid by the foot of the stapes. The fluid in the perilymphatic spaces, being bounded by bony walls, has only *one* means of escape, — the round window with its yielding membrane.

To reach it, the fluid of the labyrinth must either pass through the helicotrema, flowing over from the scala vestibuli into the scala tympani, or, as it would probably not have time to do so in the case of sonorous vibrations, press the membranous partition of the cochlea against the scala tympani. The converse action must take place when the air in the auditory passage is rarefied.

"When[1] the pressure of the fluid in the scala tympani is increased by driving the foot of the stirrup against the oval window, the membrane at the base of the arches (of Corti) will sink downwards (*i.e.* the membrana basilaris), the fibres of the second series of Corti's arches be more tightly stretched, and perhaps the corresponding places of the fibres of the first series be bent a little downwards. It does not, however, seem probable that the fibres of the first series themselves move to any great extent, for their lateral connections are strong enough to make them hang together in masses, like a membrane, when they have been released from their attachment in anatomical preparations. On reviewing the whole arrangement, there can be no doubt that Corti's organ is an apparatus adapted for receiving the vibrations of the membrana basilaris, and for vibrating of itself; but our present knowledge is not sufficient to determine with accuracy the manner in which these vibrations take place.

[1] Helmholtz, ed. 1877, or Eng. ed. 1885.

"Now Corti's fibres (pillars) are wound round and covered over with a multitude of very delicate, frail formations, — fibres and cells of various kinds, partly the finest nerve terminal fibres with appended cells, and partly fibres of ligamentous tissue, which appear to serve as a support for fixing and suspending the nerve formations. They are grouped, like a pad of soft cells, on each side of and within Corti's arches. The most important of them appear to be cells which are furnished with hairs, precisely resembling the ciliated cells in the ampullæ and utriculus. They appear to be directly connected by fine varicose nerve fibres, and constitute the most constant part of the cochlean formations; for with birds and reptiles, where the structure of the cochlea is much simpler, and even Corti's arches are absent, these little ciliated cells are always to be found, and their hairs are so placed as to strike against Corti's membrane during the vibration of the membrana basilaris."

"The essential result of our description of the ear may consequently be said to consist in having found the terminations of the auditory nerves everywhere connected with a peculiar auxiliary apparatus, partly elastic, partly firm, which may be put in sympathetic vibration, under the influence of external vibration, and will then probably agitate and excite the mass of nerves. Now it was shown . . . that the process of sympathetic vibration was observed to differ according as the bodies put into sympathetic vibration were such as, when once put in motion, continued to sound for a long time or soon lost their motion. Bodies which, like tuning-forks, go on sounding for a long time, are susceptible of sympathetic vibration in a high degree, notwithstanding the difficulty of putting their mass in motion, because they admit of a long accumulation of impulses, in themselves minute, produced in them by each separate vibration of the exciting tone. But, precisely for this reason, there must be the exactest agreement between the pitches of the proper tone of the fork and of the exciting tone, because otherwise subsequent impulses, given by the motion of the air, could not constantly recur in the same phase of vibration and thus be suitable for increasing the subsequent effect of the preceding impulses. On the other hand, if we take bodies for which the tone rapidly dies away, such as stretched membranes, or thin, light strings, we find that they are not only susceptible of sympathetic vibra-

tion when vibrating air is allowed to act on them, but that this sympathetic vibration is not so limited to a particular pitch as in the other case, and they can therefore be easily set in motion by tones of different kinds. For if an elastic body, on being once struck and allowed to sound freely, loses nearly the whole of its motion after ten vibrations, it will not be of much importance that any fresh impulses received after the expiration of this time should agree exactly with the former, although it would be of great importance in the case of a sonorous body, for which the motion generated by the first impulse would remain nearly unchanged up to the time that the second impulse was applied. In the latter case, the second impulse could not increase the amount of motion unless it came upon a phase of the vibration which has precisely the same direction of motion as itself. The connection between these two relations can be calculated independently of the nature of the body put into sympathetic vibration, and, as the results are important to enable us to form a judgment on the state of things going on in the ear, a short table is annexed: —

Difference of Pitch in terms of an equally tempered tone, necessary to reduce the intensity of sympathetic vibration to $\frac{1}{10}$ of that produced by perfect unisonance.	Number of vibrations after which the intensity of tone in a sonorous body whose sound is allowed to die out, reduces to $\frac{1}{10}$ of its original amount.
1. One-eighth of a tone	38.00
2. One-quarter of a tone	19.00
3. One semitone	9.50
4. Three-quarters of a tone	6.33
5. A whole tone	4.75
6. A tone and a quarter	3.80
7. A tempered minor third or a tone and a half . . .	3.17
8. A tone and three-quarters	2.71
9. A tempered major third or two whole tones	2.37

"Suppose that a body that vibrates sympathetically has been set into its state of maximum vibration by means of an exact unison, and that the exciting tone is then altered till the sympathetic vibration is reduced to one-tenth of its former amount. The amount of the required difference of pitch is given in the first column in terms of an equally tempered tone (which is one-sixth of an octave). Now let the same sonorous body be struck, and let the sound be allowed to die away gradually. The num-

ber of vibrations which it has made by the time that its intensity is reduced to one-tenth of its original amount, is noted and given in the second column. Now, although we are not able exactly to discover how long the ear and its individual parts, when set in motion, will continue to sound, yet well-known experiments allow us to form some sort of judgment as to the position which the parts of the ear must occupy in the scale exhibited in this table. Thus there cannot possibly be any parts of the ear which continue to sound so long as a tuning-fork, for that would be patent to the commonest observation. But even if there were any parts in the ear answering to the first degree of our table, — that is, requiring thirty-eight vibrations to be reduced to one-tenth of their force, — we should recognize this in the deeper tones, because thirty-eight vibrations last one-third of a second for *A*, one-sixth for *a*, one-twelfth for *a'*, etc., and such a long endurance of sensible sound would render rapid musical passages impossible in the unaccented and once-accented octaves. Such a state of things would disturb musical effect as much as the strong resonance of a vaulted room, or as raising the dampers on a piano.

"When making a shake we can readily strike eight to ten notes in a second, so that each tone separately is struck from four to five times per second. If, then, the sound of the first tone had not died off in our ear before the end of the second sound, at least to such an extent as not to be sensible when the latter was sounding, the tones of the shake, instead of being individually distinct, would merge into a continuous mixture of both. Now shakes of this kind, with ten tones to a second, can be clearly and sharply executed throughout almost the whole scale, although it must be owned that from A downwards, in the great and contra-octaves, they sound bad and rough, and their tones begin to mix.

"Yet it can easily be shown that this is not due to the mechanism of the instrument. Thus if we execute a shake on the harmonium, the keys of the lower notes are first as accurately constructed and just as easy to move as those of the higher ones. Each separate tone is completely cut off with perfect certainty at the moment the valve falls on the air passage, and each speaks at the moment the valve is raised, because during so brief an interruption the tongues remain in a state of vibration.

Similarly for the violoncello. At the instant when the finger which makes the shake falls on the string the latter must commence a vibration of a different periodic time, due to its length, and the instant the finger is removed the vibration belonging to the deeper tone must return. And yet the shake in the base is as imperfect on the violoncello as on any other instrument.

"Runs and shakes can be relatively best executed on a pianoforte, because, at the moment of striking, the new tone sounds with great but rapidly decreasing intensity; hence, in addition to the inharmonic noise produced by the simultaneous continuance of the two tones, we also hear a distinct prominence given to each separate tone. Now, since the difficulty of shaking in the base is the same for all instruments, and for individual instruments is demonstrably independent of the manner in which the tones are produced, we are forced to conclude that the difficulty *lies in the ear itself* [italics mine]. We have, then, a plain indication that the vibrating parts of the ear are not damped with sufficient force and rapidity to allow of successfully affecting such a rapid alteration of tones. Nay, more, this fact further proves that *there must be different parts of the ear which are set in vibration by tones of different pitch* and which *receive the sensation of these tones.*

"We may on the whole assume that the parts of the ear which vibrate sympathetically have an amount of damping power corresponding to the third degree of our table. Of course there can be no question of exact determinations, but it is important for us to be able to form at least an approximate conception of the influence of damping on the sympathetic vibration of the ear, as it has great significance in the relations of consonance."

Helmholtz means by the expression "sympathetic vibration" the vibratory response of a given structure to a determinate tone primarily, and to over and under tones secondarily. Physicists have shown that a vibrating body is sympathetically affected by tones both above and below its own proper tone, but that the sympathetic susceptibility decreases very rapidly as the scale is ascended or descended from the given note.

Helmholtz materially modifies his views from time to time as to the parts of the internal ear which vibrate sympathetically. In the first edition of his *Die Lehre von den Tonempfindungen*, he put forward the view that it was the rods of Corti

which were thus sympathetically affected, but in the fourth edition of his work he substitutes the fibres of the membrana basilaris, which, according to the measurements of Hensen and C. Hasse, he held to be admirably suited for the work. The membrane is composed of radial fibres in two or more sheets, but the fibres do not extend through the whole breadth of the basilar membrane. These sheets are covered above and below by cellular and connective tissue of no inconsiderable mass as compared with the mass of the fibres of the membrane, but which most writers, following Helmholtz, have ignored as not affecting the result. Corti's arches are now considered by Helmholtz to be merely the ways along which the vibrations are transmitted from the basilar membrane to the nerve end cells.

According to Helmholtz, the long, stiff hairs of the ampullæ are extremely well adapted for vibrating sympathetically with the motion of the fluid, and hence for producing mechanical irritation in the free nerve fibres which lie in the soft epithelium *between their roots*, as he supposed.

In the utriculus and sacculus, on the other hand, the short sensory hairs, according to Helmholtz, project into the concavo-convex covers formed of otoliths and some undetermined matter, where they are stimulated by contact with the otoliths. Helmholtz appeared to lay greater stress upon the direct action of the otolithic mass upon the *bare nerves;* for he says (*loc. cit.* p. 139): "Close to these surfaces (*i.e.* the epithelial surfaces of the maculæ utriculi and sacculi), which are covered with nerves, lie the calcareous concretions called auditory stones. In human beings the otoliths are free (*i.e.* not inclosed in a solid mass). These otoliths are also extremely well suited for producing mechanical irritation of the nerves whenever the fluid in the labyrinth is suddenly agitated. The fine light membrane with its interwoven nerves probably instantly follows the motion of the fluid, whereas the heavier crystals are set more slowly in motion, and hence also yield up their motion more slowly, and thus partly drag and partly squeeze the adjacent nerves. This would satisfy the same conditions of exciting nerves, as Heidenhain's tetanomotor, which consists of a rapidly oscillating ivory hammer, which at every blow squeezes without bruising the nerve."

Our author further says (p. 151): "If we maintain that every nervous fibre hears in its own special pitch, we should have to conclude that the vibrating parts of the ear, which convey these sensations of the highest tones to the ear, are much less sharply defined in their capabilities of resonance than those for deeper tones.

"This means that they lose any motion excited in them comparatively soon, and are also comparatively more easily brought into a state of motion necessary for sensation. This last assumption must be made, because for parts which are so strongly damped the possibility of adding together many separate impulses is very limited, and the construction of the auditory cilia in the little bags of otoliths seems to me to be more suited for this purpose than that of the shortest fibres of the basilar membrane. If this hypothesis is confirmed, we should have to regard the auditory cilia as the bearers of squeaking, hissing, chirping, crackling sensations of sound, and to consider their reaction as differing only in degree from that of the cochlear fibres."

The vibrations of the membrana basilaris cochleæ Helmholtz describes in the following manner: —

"The mechanical problem here attempted is to examine whether a connected membrane with properties similar to those of the membrana basilaris in the cochlea could vibrate as Herr Hensen has supposed this particular membrane to do; that is, in such a way that every bundle of nerves in the membrane could vibrate sympathetically with a tone corresponding to its length and tension, without being sensibly set in motion by the adjacent fibres. For this investigation we may disregard the spiral expansion of the basilar membrane and assume it to be stretched between the legs of an angle of the magnitude of 2η."

Here follows an extended mathematical computation of the amount of vibration of such a membrane, for which the reader is referred to Helmholtz's treatise.

The membrane assumed is perfectly uniform in structure in all its parts, is tensely stretched in one direction, its transverse, but not so in its longitudinal direction. Under the conditions of the calculations (which Helmholtz assumes may be those conditioning the cochlear organ), each simple tone sets in vibration only some narrow strips of the membrane in the direction

at right angles to the plane of the membrane, every fibre of any strip vibrating practically independently. He claims to show by this mathematical analysis that every excitement of a bundle of transverse fibres by the respective fundamental tone must be accompanied by weaker excitements of the unevenly numbered harmonic undertones, the intensity of which would be multiplied by the factors $\frac{1}{9}$, $\frac{1}{25}$, and generally $\frac{1}{m^2}$. This hypothesis, advanced by Riemann in his *Musikalische Logik*, is considered by Helmholtz to be tenable, though nothing of the kind is observable in the ear. Helmholtz states that probably the appendages of the basilar membrane greatly impede the formation of tones with nodes.

Paul Meyer has given special attention to the structure of the basilar membrane among the Sauropsida, and he finds that among most reptiles it is composed not of a series of parallel fibres, but of a homogeneous plate of substance, and he is sure that in no case will it allow of the interpretation placed on this structure in the Mammalia; and he concludes after this study of the basilar membrane in reptiles and birds and a consideration of the facts and theories of other writers, Helmholtz especially, that "une membrane fort peu élastique d'une épaisseur très appréciable superficiellement striée, composée de diverses couches, dont, disons-le en passant, l'épaisseur relative varie avec l'âge, tel est, en dernière analyse, l'appareil aquel on voudrait rapporter nos plus fine sensations auditives." "Ainsi donc, pas plus que l'organe de Corti que la membrane de recouvrement, la membrane basilaire ne répond aux conditions necessaire pour servir de base."

Owsjannikow (p. 11) did not find (in his studies on Petromyzon) that the hair cells were nerve-end cells, but concluded that the nerve fibres ended freely in the basement membrane under the sensory epithelial cells. This concerns us here only in so far as it influenced his physiological conceptions of the *modus* of the transmission of the vibratory motion from the endolymph to the nerve fibre. Owsjannikow believed that the sensory cells (*i.e.* in Petromyzon) did not possess auditory hairs.

"Ein solcher Zusammenhang [*i.e.* between nerve and hair cell] ist kaum nöthig. Nehmen wir an, dass durch irgend einen Ton die Endolymphe in Bewegung gesetzt wird und die Wellen

an das Cylinderepithel anschlagen, so werden sie unstreitig durch den Stoss erschüttert. Die Erschütterung pflanzt sich weiter fort von den Cylinderzellen auf die Grundmembran und von dieser auf den Nerv, der mit seiner Spitze unmittelbar an dieselbe sich anlegt." In this way, says the author, the transmission of a tone to the nerve would occur in a very simple manner without the necessity of recourse on the part of nature to a more complicated structure.

In 1876, Lavdowsky (178) published his physiological conclusions, which were based not on actual physiological experiments, since, says he, microphysiological experiments on the cochlea of warm-blooded animals are almost impossible, but on a careful analysis of the structure and composition of the organs in question; while the only experimental basis to serve as guiding light was the well-known experiments of Hensen's on the Decapod ear, and Ranke's on the otocysts of Pterotrachea, with the demands which the physiological acoustics make on the auditory organs of tone perception. The demands of acoustics, according to Lavdowsky, may be stated under three heads. In order to account for audition there must exist in the auditory organ, as our author conceives it, three mechanisms. They are

1st. A vibration mechanism, capable of responding to and very sensitive to vibrations of the surrounding medium.

2d. A percipient mechanism.

3d. A regulation mechanism or damping apparatus.

Since, however, it is impossible to separate the cochlea from the rest of the canal complex when considering the physiology of audition, it necessarily follows that one must use hypotheses to satisfy the demands of acoustics.

This investigator considers that the cochlea performs one function, the rest of the ear the other of the two functions assumed to belong to this organ; and the former, he says, is the most important one belonging to the ear.

The whole of the ear, save the cochlea, subserves the function of simple auditory perceptions, while the cochlea subserves the double function of a tone differentiator or analyzer, as well as that of sound perception. The utriculo-sacculus and semicircular canals perceive the qualitative differences existing between various forms of motion, *e.g.* light and sound waves, but cannot perceive, except in the most general way, the character of a mass of tones or a musical picture.

The cochlea, on the other hand, thanks to its more differentiated and complicated structure, is able to separate a musical picture into its several parts, to perceive the tonal differences, such as pitch and timbre, and it is probably the place where rustling sounds are distinguished.

These functions are performed by the following parts. In the utriculo-sacculus and ampullæ, by the auditory hairs and the parts they are supported by. In the cochlea, by the associated fibres of the basilar membrane and hair-bearing cells and arches of Corti, the percipient elements being the hair cells which are directly continuous with the nerves. The indispensable sensitiveness or delicacy of perception in the cochlea finds a suitable physical basis in the capsules of Hensen, which, like sense buds, represent organs which are sensitive in the highest degree to the purely mechanical stimuli of sound waves.

A special analysis of the other parts of the cochlea shows us that in the basilar membrane, from its position, its character, and composition, — being made of straight, elastic fibres somewhat like strings tensely drawn between the two scalæ, — we have a vibration mechanism, which, as Helmholtz has already shown, is highly capable of vibrating. The vibrations of its fibres must be very regular, though naturally in different parts of its course they would be of varying intensity — that portion on which the hair cells lie being the most active in its movements, *i.e.* having the greatest amplitude, since this part is least loaded and has freest motion. This motion is sufficient to communicate to the hair cells the requisite stimuli for hearing. The abundance of basilar fibres, of which five hundred are allotted to a half-tone in the human ear, compels us to assume that they fall naturally into smaller or larger groups. This, as we know, agrees with their anatomical relations, which are responsive to various tones, the lowest of which are found near the apex of the cochlea, while the highest tones are perceived at the base. This calculation is based solely upon their length, their varying thickness and the amount of load in the shape of surrounding tissue carried being left out of consideration.

However these things may be, we have in the cochlea, as everything leads us to believe, the basilar membrane as the *vibration apparatus* demanded by physiological acoustics, and the hair cells with their capsules as the *percipient elements*.

Nevertheless there are observers who will not admit that such can be the function of the basilar membrane, *e.g.* Paul Meyer, who calls attention that among the lower vertebrates, — viz. among the Reptilia, — the basilar membrane has the structure of a homogeneous plate; and besides, the membrane is too thick and not elastic enough among the Mammalia to serve the purposes intended. According to Meyer, the hairs alone perform this function.

If this was correct, it was argued that it would be impossible to account for the formation of the basilar membrane. Keeping the gradual development of the auditory sense in mind, it follows that we must look for greater perfection of the anatomical basis, for the two must go hand in hand. Most of the perfecting changes have taken place in the cochlea. The arch of Corti appears first among mammals, and the second row of strings as well as the fourth row of hair cells, and perhaps many other things which have remained undiscovered. The hair covering of these cells *is very different from what is found among lower vertebrates* (the same is true of the auditory hairs of the rest of the canal complex). When one remembers that in such animals (fishes, Amphibia, and in part also birds), in contradistinction to the weak development of the basilar membrane, the hairs show a very prominent development (*e.g.* cupula terminalis, etc.), when we consider all these things, Meyer's objections are satisfied, and furthermore, it is not too much to hold that the basilar membrane and auditory hair cells *undergo reverse processes of growth* and are perhaps dependent upon each other to a certain extent.

But what is the significance of the hairs in the auditory apparatus as a whole, and specially in the cochlea?

Considered in organic continuity with their bearers, the cells, they can hardly be separated from the latter in their significance as percipient elements; but in the case of the cochlea, *where only bars — bacilli, and no hairs in the proper sense — are present*, it is necessary to limit the amount of their sensitiveness to sound waves. One is forced to conclude that owing to their unusual shortness and relative thickness they are scarcely capable of regular vibrations. Helmholtz assumed that structures strongly damped would be relatively more strongly affected by blows of short periods and streamings of the endolymph than by musical tones.

The third demand of physiological acoustics is satisfied by the membrane of Corti, which acts as a damping apparatus. Its constitution and position and all its peculiarities speak for this view of its function. It is a most delicate damping apparatus. By each change in the endolymph the damper is pressed down upon the ends of the hair cells, and in this manner regulates above everything else the rustling noises, which might impair the purity of the musical tones.

We hear with the vestibule; we understand with the cochlea. The cochlea is, then, not so much an organ for simple audition, but more for the complicated processes of the differentiation and perception of musical tones.

The part played by the central nervous system in audition is not considered by Lavdowsky, since it lies beyond the scope of his paper.

Meyer is thoroughly convinced that the hair-bearing cells, and they alone, subserve the auditory function by being sensitive to vibrations and transmitting them to the central nervous system, as he explains in the following words, already referred to in the account of Lavdowsky's views: —

"Ces cils (les crins des ampoules et les pinceaux du saccule) relativement assez épais, raides, vitreux, cassants, semblables en quelque sorte à des verges de verre ou d'acier, formant par leur insertion à peu près linéaire des faisceux minces, eux-mêmes fixés sur une sorte de plateau du même nature, indépendant du protoplasma de la cellule qui les porte, ces cils ne doivent-ils pas présenter au plus haut degré la propriété de vibrer pour leur compte, de vibrer par influence pour un ton déterminé? ne constituent-ils pas, en un mot, un appareil de resonance presque mathématique, une sorte de diapaison, infiniment superieur dans tous les cas à ces cordes basilaires auxquelles la theorie de Hensen voulait faire jouer le même rôle? à une theorie solide de la perception des sons, et déjà, par exclusion nous arrivons à chercher la clef du problème dans le seul élément du limaçon que nous n'ayons pas encore soumis à une étude physiologique rigoureuse, dans les cellules auditives elles-mêmes."

Hensen, while agreeing in general with Helmholtz's account of the auditory physiological processes, gave the following description of the manner in which he conceived the parts of the

organ of Corti to act during the perception of auditory stimuli that is under the mechanical influences of the transmitted wave motions: —

"Wenn Abschnitte der Basilarmembran durch, ihren Breitenverhältnissen entsprechende, Töne in Transversalschwingungen kommen, wird nothwendig die Papilla sich entsprechend bewegen. Die membrana Corti dagegen kann von der Schwingung nicht berührt werden, denn sie ruhrt nur denjenigen Zellen direct auf, die sich der Lamina ossea stützen. Es werden also die Stäbchen lockerer oder fester (zuerst die der äusseren Zelle?) trotzt ihrer schwachen, fast federnden Unterlage gegen die Masse der Corti'schen Membran gepresst werden. Es fragt sich aber weiter, namentlich meinen Erfahrungen an Krebsen gegenüber, wie durch das Anpressen oder Entlasten der Stäbchen eine Empfindung erzeugt werden kann. In dieser Beziehung ist an das auffallende Verhalten der Corti'schen Zellen zu erinnern, die so leicht aus der Lamina reticularis sich scheinbar intact loslösen und doch dabei ihre *Endplatte mit den Stäbchen* darauf in der Lamina reticularis zurücklassen. Diese Endplatte scheint demnach so selbständig zu sein, dass sie auf den Inhalt der unterliegenden Zelle einen Druck ausüben kann. Ist nun die Corti'sche Zelle eine Endganglie, so ist zugegeben, dass die wechselnde Spannung ihres Inhaltes zu einer Empfindung Anlass geben kann."

As already explained in the section on the morphology of the cochlear organ, Hensen found an ovoid body in the upper end of the hair cells which he considered as the nerve end organ within the hair cell. He was inclined to compare this structure with the touch corpuscles, end knobs, and Pacinian bodies of other tissues so far as generalities were concerned.

He considered the function of this mechanism, which, according to his view, is the percipient element *par excellence*, to be brought into play in this manner. The hair cells over a certain number of basilar membrane fibres — the number and location of the fibres being determined by the pitch of the tones transmitted to the ear — were moved up and down with and by the length of the excursions of the basilar fibres. The hair cells are thus thrust abruptly against the membrana tectoria, and the short auditory bacilli driven forcibly into the cell and against the ovoid nerve end body, which thus stimulated transmitted the impulse, causing an auditory perception.

As is well known, sound waves falling on a telephone plate cause it to vibrate. An electric current is propagated to the distant plate and causes it to repeat the vibrations of the first plate. There is *no analysis* of sound waves by the second plate. With these fundamental facts of the action of the electric telephone in mind, Rutherford (1886, 246) invented what he terms his "Telephone Theory of Hearing." I give below the gist of his statement of the theory.

The hairs of the cochlea do not vibrate sympathetically, but they, all of them, vibrate to every tone which enters the cochlear canal, as does the tympanum. There is no analysis of tone produced by complex vibration, either in the cochlea or the part of the external ear. The hair cells transform sound vibration into nerve vibration similar in frequency and amplitude to sound vibrations, and these simple and compound vibrations of nerve energy arrive in the sensory cells of the brain and there produce not sound again, of course, but sensations of sound, the nature of which depends not on the stimulation of different sensory cells, but on the frequency, amplitude, and form of the vibrations coming into the cells, probably through all the fibres of the auditory nerve.

This theory carries the physical cause of discord and harmony into the brain, and the mathematical principles of acoustics find entrance into the obscure region of consciousness.

Now if nerve energy were only electricity, we might accept this theory at once, but nerve energy is very sluggish as compared with electricity. Rutherford tells us that he kept back his theory for five years because he thought there was no possibility of sending a rapid series of vibrations along a nerve.

If we give to a motor nerve of a Frog 10 electrical shocks per second, there will be produced 10 contractions in the muscle per second; if 40 shocks, not 40 contractions, but *one continuous contraction*, on account of the fusion of the several contractions.

Now if we listen to such a muscle, we hear a musical note having the pitch of 40 vibrations per second. Each sound vibration results from the sudden shock of a chemical discharge, due to the arrival of each nerve impulse in the muscular substance. If we stimulate with a rapidity of 200 times per second (by means of a tuning-fork apparatus) the pitch of the muscle

note corresponds. Our author sent as many as 352 shocks per second into a nerve, and hence sent 352 pulses along the nerve, and got the note 352 V^b per second, which equals F on lowest treble clef. He could not get higher notes than this, only noise.

Bees' wings go at rate of 460 vibrations per second; hence their muscles contract the same number of times per second; this would give us A in treble clef.

Rutherford says if his theory was accepted, it would lead to a reconstruction of the physiology of the other sense organs.

Pritchard states his views of the function of the rods of Corti and of the parts of the ear in the following manner. After saying, "It appears evident that those investigators had not suspected, much less discovered, the fact that the rods are most exquisitely graduated; for otherwise they could surely never have doubted that as beautiful and suitable an apparatus could have any other ostensible purpose than that of appreciating the various sounds," our author concludes that "this uniform graduation of the rods presents to my mind so plausible and reasonable a key to their use that there can scarcely be a doubt as to their real function. I consider that the cochlea as a whole represents a finely constructed musical instrument, similar in nature to a harp or musical box, the strings of one and the teeth of the other being represented by the rods of Corti. The spiral, bony lamina is nothing more nor less than a natural sounding-board, in connection with the end of which are arranged the rods." The course of the vibratory stimuli from the endolymph to the brain is, according to Pritchard, the subjoined. The vibrations are taken up from the endolymph by the rods of Corti, and transmitted to the nerve end cells, which he considers are present in the form of the so-called Deiters's and Corti's (as well as others) cells. From these the motion makes its way down the nerve to the brain. After entering the ear from without, Pritchard thought all sounds were perceived by the vestibular portion of the labyrinth, but merely as sounds, the direction discovered by the semicircular canals; but the pitch and timbre, or, as he says, the "note," of the sound is perceived by the cochlea alone. Here the motion, after passing through the fluid of the cochlea, "probably strikes the lamina spiralis, which, acting as a sounding-board, intensifies and trans-

mits the vibration to the system of rods. There is doubtless a rod, not only for each tone, or semitone, but even for much more minute divisions of the same, so that every sound causes its own particular rod to vibrate.

As the foregoing amply indicates, students of auditory physiology, especially that of the cochlea, have thus thought along two sharply defined lines, the one school holding that the rods of Corti, the fibres of the basilar membrane or other of the non-sensory structures, were the percipient elements, while the other school claimed that the nerve end hair cells, by means of the hairs which they put forth, are alone the percipient elements. The rods of Corti were made to do duty as the percipient structures by Helmholtz in his earlier studies, because the hair cells, as such, had not been discovered by Corti or his immediate successors, and they looked upon the rods as the essential elements of the organ. The basilar membrane (fibres) was afterwards substituted by Hensen and at once adopted by Helmholtz, because from their insufficient knowledge of its structure, it appeared not only admirably suited but apparently specially designed for this very function. Hasse for the lower vertebrates, and Meyer for the whole group, denied this function to the basilar membrane, because they found animals with a cochlea without a suitable basilar membrane, but supplied with hair cells.

The subject has never been explained with lucidity from the comparative anatomical standpoint, and so the Hensen-Helmholtz "piano-string" theory has held the field against all comers. Although some students, like Foster, considered it inadequate, and others, like Rutherford, not content to leave matters as they were, offered new solutions of the difficulty, it is not probable that any general advance could have been made in physiological ideas in this field until a broader view of the whole matter had been taken, based upon increased anatomical and embryological knowledge.

It is a necessary consequence of the canal organ parentage of the ear sense organs, that they inherit functions similar to those of the parent organ, modified only in individual ways, as offspring always are modified in some degree.

The great similarity, on the other hand, of the offspring, among themselves and to their parent, would enable any one of them to take on the functions of one or more of its fellows —

more especially nearest kin — in case it or they were in any way hindered from performing the proper function to its full or even a sufficient extent, — *e.g.* as when the sensory hairs are loaded down with otoliths. Indeed, so far as the auditory function is concerned, one sense organ might be made to serve all the auditory needs of the animal; and, had not the inherited tendency to divide compelled the primitive vertebrate ear to progress by the further division of its auditory sense organs, in all probability no such canal complex as exists in most forms would ever have been produced; but the enlarging physiological necessities might have been met by the differentiation of the original establishment, after much the same plan we find followed by the mammalian cochlear organ in its development, or of the retina in the eye. As an instance of the moulding influence which the view heretofore held of the relation of the two prime chambers of the ear to each other, exercised not alone on morphological ideas, but physiological as well, I may cite Paul Meyer's statements, made in harmony with the earlier ones of Hasse, that the accepted division of the auditory vesicle into superior and inferior parts was no less important for physiology than for anatomy. The superior part had, by entering into more intimate relations with the bony walls of the cranium and the reduction of its perilymphatic spaces, acquired the (or restricted its) function to the perception of vibrations transmitted through the bone, while the inferior part, by entering into intimate relation with the tympanic transmission apparatus, and by the enlargment of its perilymphatic spaces, has acquired the (or enlarged its) function to the perception of vibrations coming through the tympanic apparatus. This differentiation has become the more perfect by the almost complete separation of the two parts from one another.

Such are Hasse's and Meyer's views; but I have shown that in vertebrates as low as the Elasmobranchs, the utriculus and sacculus are nearly as completely isolated as in mammals, and furthermore, after the general consideration of the relation of canal organs to the surface of the body (their relation to the close investment by membrane bones, as in fishes, included), it does not seem to be a specially pregnant idea that the sense organs of the semicircular canals and the utriculus are only capable of, or are restricted to, the perception of vibrations

transmitted through the investing cranial bones. Not that it is denied that such transmission of vibrations through the cranial bones may take place, but there is neither physical nor morphological basis for the conclusion that the two parts of the ear are not subject to all vibrations affecting the ear from whatever source, in quite equal degree. It is certainly not made clear on physical grounds by Meyer nor his predecessors in this view, Hasse, Lucae, Mach, Politzer, and others, nor by his successors, more especially and recently Hensen, how the vibrations affecting the cranial bones are transmitted to the utricular section of the canal complex more than to the saccular section, and there is no mention of anatomical arrangement of the parts adequate to the work of insulating the cochlea or any other part of the saccular region from these vibrations. So far as our knowledge extends at the present day, the only conditions affecting the activity of the sense organs is the greater or less perfection or specialization of the sense organs themselves, in the direction of greater or less sensitiveness to stimuli, differing in pitch, intensity, and other qualities, if such there are.

As Hasse had already shown, and as Meyer notes as an interesting condition, the perilymphatic spaces of Chelonians is so large and extensive that any vibration whatsoever, arriving at any part of the surface of this sac, would be transmitted equally well to all parts of the internal ear.

From a general standpoint, it is evident that there is no peculiar or special kind of wave motion (vibration, undulation) which alone is entitled to be called sound wave; for all so-called sound waves may (produce) give rise to sensations *other than those of hearing*. And those vibrations of the atmosphere which serve to cause the sensations of hearing in the ears of one individual may entirely fail of that effect in the ears of another. We have a so-called musical scale within whose limits all possible sounds must fall, as far as concerns their pitch; but since some ears are not sensitive to low notes, and others deaf to high-pitched notes, it follows that there is no rigid auditory scale, and consequently no sharp line of demarcation between genuine auditory and tactile stimuli when caused by disturbances in the supernatant fluid of the sense organs of the ear on the one hand, and of the surface of the skin on the other.

All *sound* waves are taken up from the endolymphatic liquid;

and it is just as incorrect to speak of our hearing the vibrations of the air as it would be to say that we hear the vibrations of the string or bar or tongue or other music (sound) producing instrument without mediation. At all times and under all circumstances vertebrate animals have *heard*, if at all, by means of disturbance of sensory hairs projecting from the morphological surface of the body into the water in which they lived. Now, in the lower forms, *e.g.* some fishes, the essentially sac-like ear is open to sea-water, and when the outer opening was finally closed, it must have been in some form whose ear was at one time open to the supernatant water; so that it is more than a figure of speech to say that before emerging upon land the vertebrate type fitted its ear for the step by shutting up the outer opening of the endolymphatic duct, thereby retaining and perpetuating an aquatic condition essential for the surviving sense organs of the auditory type. Indeed, these auditory organs owe their survival to such closing up of the auditory sac and to a sufficient and permanent supply of a watery medium for the support of the sensory hairs. This is due to the fact that it is impossible to construct so delicate a mechanism to operate in the air. The organ arose in aquatic ancestors, and the physical requirements remaining the same, the organ must of necessity acquire a liquid chamber in the head to replace that originally supplied by the sea.

Wherein does the difference in the physiological function of the auditory sense organs consist? Does it lie entirely in the structural differences between the various organs of the auditory complex or entirely in the structural differences of the central terminations, or in both combined?

The general consensus of physiological opinion at the present day is in favor of the third view. As every one knows, the sense organ may be cut off from its central connection, and still the characteristic sensation be felt, and the central organ may be so destroyed that although the sense organ and its centripetal conductors are intact, still under stimulation no sensation may be aroused. It is evident, I think, that we shall never be quite certain that a difference in structure of the sense organ *necessitates* a difference in physiological functions until we shall succeed in grafting on to the nerve of one special sense the sense organs belonging to another special sense, as, for example, in-

graft the nose of a fish upon the auditory nerve, and determine if the fish may not be able to hear through the mediation of the *hair cells of the nasal epithelium*, — a feasible operation, which promises valuable information to the successful operator. The grafting of the ear upon the nasal nerve would in all probability not be a success, on account of the protected condition of the sensory cells. This protected condition of the auditory hair cells may be in part due to an attempted exclusion of all sensory impulses, save those of vibratory motion of the water; at any rate, such exclusion follows as a consequence of the inclosure of the organ.

Foster (1891, 92), *loc. cit.* p. 1213: "If the organ of Corti is the means by which we appreciate tones, it is evident that by it also we must be able to estimate loudness, *for the quality of a musical sound is dependent on the relative intensity, as well as on the nature, of the overtones* [italics mine]. And since noise is at best but confused music, the cochlea must be a means of appreciating noises as well as sounds. But this would leave nothing whatever for the rest of the labyrinth to do in respect to the appreciation of sound, save so far as the difference in structure between the hair cells of Corti, with their short thick rods, and the hair-bearing structures in the maculæ and cristæ, with their thin delicate hairs, may possibly indicate a difference of function, the latter being more susceptible to the irregular vibrations of noises."

The physiological rôle of the utricular sense organs is very inadequately understood, but owing to the primitiveness of the histological characters of the sensory plate and its entire agreement in structural details with the ampullar sensory epithelium, it is probable that they retain their primitive function; at least such a view is allowable until it is shown that the function has changed more than the apparent structure. I have nothing to add to what has been written on this subject by Hasse, Hensen, Meyer, and Retzius, except to offer the view that the otoliths do not play so important a part in the function of this sensory apparatus as has been commonly held, and to insist upon the proper allowance being made for the increasing refinement and sensitiveness to given stimuli that the auditory nuclei of the brain must undergo in connection with the ever-growing association mechanism. Granting this fact its full and proper influ-

ence, it does not become necessary to add a morphological increment to the nerve end organs each time the functional powers of the *sense* is increased; for just as the trained eye can separate the component colors and forms and correctly judge of their relations in a picture, or as the trained nose can separate the several odors of a compound perfume and may correctly judge of the relative proportions in which the ingredients are mixed, unaided by any other sense, or just as the trained ear can resolve a musical chord into its notes without having gained during the training any morphological increment in the end organ; so it is entirely possible to build up the complex auditory function of a bird, for example, without modifying the structure of the end organ in any considerable degree. In this direction we may look for the explanation of the wonderful acoustic powers of the thrushes with their undifferentiated cochlear organs.

It certainly cannot be true, as Paul Meyer states, that the macula utriculi is the only acoustic organ of his "pars superior," nor that it is in any sense the physiological centre of this group of sense organs.

The sacculus, although belonging to the *pars inferior* auct., has never been the subject of experimentation, as have the canals, utriculus and cochlea. Its function has always been assumed to be that of the perception of noises, in common with the utriculus. So far as its morphological relations are concerned, it is perfectly evident that its function in any given group of animals must be practically identical with that of the utriculus, unless — and here is the density of our ignorance exposed — unless the central end connections in the case of the two organs are so different as to cause different psycho-physiological phenomena from identical stimuli. I think the nerve connections indicate the latter view as nearer the truth.

As for the larger question of the function of the utriculo-saccular organs and their derivatives throughout the vertebrate series, Milne-Edwards grasped the subject in its entirety and pointed out the only possible way to a solution many years ago. He said, in his great storehouse of facts (*loc. cit.* p. 76 *et seq.*): "Ainsi que je l'ai déjà dit, les Poissons sont également dépourvus de la portion cochlienne de l'oreille interne, dont le rôle parait être des plus importants chez les Vertebres dans l'appréciation

des intervalles musicaux et du timbre des sons. Il serait par conséquent intéressant d'examiner si les Poissons sont sensibles au bruit seulement, ou si ces Animaux sont capables de distinguer les différences de ton et de timbre ; *mais je connais aucun fait qui nous permette de trancher la question*" [italics mine].

The field for experiment is as open to-day as when Milne-Edwards reviewed the subject.

Although Exner believed that the organ of Corti was capable of perceiving not only tones but all other noises as well, Hensen held to the doctrine advanced by Helmholtz, according to which the cochlear organ was capable of perceiving tones only. As to Töpler's experiments with the electric spark, which gives only a single, short, sharp impulse to the air, or it snaps, as we say, Helmholtz concluded that such a snap could not possibly give rise to an irritation of the cochlear apparatus ; indeed, a series of such snaps would not give rise to a tone unless they followed each other with a considerable degree of rapidity. But it is found that an increase in the rate at which the electric sparks followed each other caused a like elevation of the pitch of the sound, and as Hensen truly says, "Diese Erfahrung würde entweder denn doch auf die Betheiligung des klangempfindenden Apparates deuten, oder sie würde auf einen zweiten Apparat, der gleichfalls Höhen — und Tiefenempfindung hervorzurufen vermag, zu beziehen sein. Zwei verschiedene Endapparate von Sinnesnerven, welche beide die gleiche Empfindung der Tonhöhe hervorrufen, stimmen nicht mit unseren Kenntnissen von den Sinnesorganen überein und widersprechen den 'Gesetzen der specifischen Sinnesenergie.'" Hensen then proceeds to explain how the basilar membrane fibres might take part in the perception of such snaps. After what I have said in the morphological part, it needs no special explanation to make clear that there is no such sharp and fundamental separation of the auditory sense organs, as regards their functions, as Hensen here assumes.

Whatever differences in the powers of tone perception there may be between the various sense organs of the ear, there can only be differences of degree, and not of kind. In my mind there exists no doubt that *the cochlear organs perceive all kinds of sounds.*

When Hensen asserts that the perception of the pitch of tones does not necessarily immediately concern the cochlear organ

(Klangapparat), it seems to me he contradicts important statements made in the preceding pages of his work. For he holds — as almost every one else does — that there are three determining physical conditions to the production of tone stimuli; viz. the pitch, or rate of vibration; the intensity, or amplitude of vibration; and the timbre, or the complexity of vibration; and furthermore, it is the essential part of his theory that the basilar membrane fibres repeat as near as may be the rate, intensity, and complexity of the waves which cause any given tone sensation. For how could the basilar membrane otherwise analyze tonal waves, and would our author have us look for another apparatus to perceive the very thing that determines the selection of the waves in the cochlea? To say, then, that the rate — or the condition which determines whether a tone is a "low" or a "high" one — does not immediately concern the cochlear apparatus is to deny that the basilar membrane vibrates sympathetically to tone stimuli, which contradicts the corner-stone of the Helmholtz theory.

Hensen cites J. Müller's dictum that "Jeder Ton erweckt sein besonderes Gefühl," and says that the tonal pitch does not play any immediate part in awakening this special sensation. He says, further on, "Ob daher die Höhe und Tiefe des Tons eine einfache Empfindung und nicht vielmehr ein complicirterer Act, bei dem das Gedächtniss wesentlich mitwirkt, eine Wahrnehmung ist, erscheint noch zweifelhaft."

In this conclusion our author begs the question; for while there is not the slightest doubt that the inadequately understood cerebral operations play an important part in all auditory perceptions, we must, while we are considering the physical basis of sound, confine ourselves to this alone; for the moment the co-ordinating apparatus is introduced into the problem it becomes altogether too complex to deal with at this time; on the other hand, we may reasonably expect to get some important facts by studying the effects of physical auditory stimuli from the physical standpoint.

Hensen feels compelled to seek for two distinct apparatuses in the ear: one for tone perception, another for other forms of sound, and the theory of the analysis of sound waves is at the bottom of it all.

The Organ of Corti, or the Mammalian Cochlear Organ.

The development of the cochlear tube precedes that of the ultimate cochlear organ by a long space of time. The continuous but very gradual differentiation of the cochlear organ in the vertebrate series above the fishes would, from the morphological standpoint, argue a gradual increase in the physiological function, and the rapid acquisition of length by the canal, as well as the wonderful complication of structure in the sense organ contained, certainly points to an important functional activity; but when we attempt to determine the character of the function and its mechanical execution, we meet with almost insuperable difficulties. As I have indicated, none of the theories yet put forward are sufficient to explain the facts, and every one of them is antagonistic to some important morphological relation, which must invalidate the arguments in greater or less degree.

The ability which many animals with a simple type of cochlear organ display in appreciation of the value of the musical quality of sounds, noises, tones, and their remarkable facility in perceiving the minutest variations in the intensity, pitch, timbre, and other tonal qualities, render any arguments as to the increase of physiological activity, based on a greater complexity in structure of the cochlear organ, not only valueless, but misleading. Our knowledge, especially of the function of this part and the nerve-end relations, is very imperfect — more so, I fear, than most students appreciate; but I do think that it is a subject which proper experimentation may and will overcome in the, let us hope, *near* future. Much depends upon our ability to decide definitely what the function of the canal sense organs is, for on the determination of this problem depends the solution of all the physiological problems of the internal ear. The direct connection of the tympanic conducting apparatus to the perilymphatic spaces which surround the saccular chamber or its derivatives in varying degree in the different groups of vertebrates, is a character of considerable physiological importance, but not deserving of such weight as Hasse and Meyer are inclined to attribute to it. For although in the Amphibia the whole saccular perilymphatic chamber is directly connected with the columella, and in reptiles the sacculus and the base of the cochlea are thus connected, and in the birds and mam-

mals the cochlear chamber alone has this relation to the auditory chain of bones ; still, when we consider the high rate of transmission of sound waves in liquid, all parts of the ear must receive the stimulus of any given set of sound waves at practically the same time.

The rate of transmission in water, which is certainly less than that of the endolymph, is five times as great as that in air.

It has been very generally assumed that when a sound wave strikes the tympanum, with the mechanical consequence that the membrane of the fenestra ovalis is forced in, the membrane closing the scala vestibuli at the fenestra rotunda is forced outward, owing to the propagation of the wave motion from one scala, through the helicotrema, into the other.

In this explanation it is entirely overlooked that the endolymphatic duct places the ear in communication with the lymph spaces about the brain, and that consequently wave motion, propagated either through the scala vestibuli or tympani, either singly or together, does not necessarily in the first case, and cannot in the second case, be transmitted beyond the helicotrema ; for any pressure increase in the endolymph is at once relieved by the progression of the stress through the endolymphatic duct into pericerebral lymph spaces. As we ascend from the lower to the higher animals, the blood pressure increases progressively ; and since the ear lies within the tissues of the animal, in fact within a lymph space, and its walls are sufficiently thin to allow of ready transmission of pressure changes, it follows that the endolymph is always subject to a stream of rhythmically variable pressures, travelling from within outward — which must be overcome by the sensory waves from without.[1] I do not refer to the rapid vibrations which occur in the body with every heart-beat and muscular contraction, and which for the most part give rise to veritable sounds to be *heard* by *attention* to them, but only to the condition of a varying pressure in the lymph space (which of course is not so great, either in its amount or its variations, as in the arteries or the veins), which must affect the entrance of sound waves from the lighter medium, the air. I find no better explanation of the perfection of the tympanic transmitting apparatus than the physical neces-

[1] See Recapitulation F.

sity of overcoming these changed conditions of pressure in the ear by thus artificially increasing the intensity of the external stimuli.

The auditory impressions gain access to the sensory structures only by the propagation of the wave impulses through the wall of the cochlear tube; and since the membrana Reissneri is much the thinner and less resistant of the two walls through which it is possible for the stimuli to pass, it is probable that it is upon the surface of this membrane only that the waves impinge which are to give rise to auditory impressions.

This is rendered all the more probable from the fact that the auditory hairs are directed upwards, inwards, and backwards (with reference to the axis of the cochlear tube), and are thus disposed in positions very favorable for the reception of wave motion progressing up the cochlear tube.

The basilar membrane, owing to the fact that it is heavily loaded on both sides and tensely drawn, does not in all probability vibrate under the influence of such delicate stimuli, *i.e.* permit their passage into the endolymph. For the moment let us admit for the sake of the older view that the basilar membrane may vibrate. It is still just as true that the stimuli are sent into the sensory apparatus from the wrong side, from within and not without, as is the case with all other known sense organs where the stimulation progresses from the sensory hair or rod through the cell into the nerve. Again, the auditory hairs of the cochlea, as I have proved them to exist, are incalculably more delicate agents for the picking up of and transmission of mechanical stimuli such as audible undulations of the endolymph from any source whatsoever.

In order to determine the physical characteristics of the hair band as a structure capable of sympathetic vibration, we tried a series of experiments on the ears of the Pig and Cat. The os petrosum was removed from the skull immediately after death and transferred to aqueous humor until it could be opened. This was done in each case as soon as possible. The cochlear eminence was removed from the petrous mass and the roofs of the several spires removed, thus exposing the membranous ductus cochlearis entire. The dorsal and outer walls were then cut away, the lower cut being made along the outer edge of the sulcus spiralis externus, and the upper cut along the insertion

of the dorsal edge of the membrana Reissneri. The whole of the stria vascularis and the membrana Reissneri are thus easily removed, leaving freely exposed the cochlear organ intact. The limbus spiralis is then easily detached with needles by puncturing along the course of Rosenberg's canal, so that the spiral papilla on the basilar membrane may be transferred to slide and cut into pieces more or less complete circles. The whole under one cover is mounted in serum and the edges of the cover glass painted with cement to hinder evaporation. The microscope with this preparation is placed in a position favorable to the transmission of vibrations to the liquid, and it is then seen that the fibres of the hair band vibrate under the influence of tones given off by the piano or a tuning-fork.

Our experiments were successful in showing that the hair band as a whole is violently agitated by loud tones, but not conclusive as to localization of tones of different pitches in different parts of the hair band. Owing to the conditions of the experiment it could not be determined that the basilar membrane was affected by the vibrations.

When such a preparation is placed on the stage of a microscope isolated in such a manner that sonorous undulations can reach the slide surface from the air alone, we have placed the hairs under conditions which severely test the delicacy of their powers of responding to the slight disturbances of the atmosphere produced by musical instruments such as the piano, violin, or horn. All of our experiments were performed with the aid of a piano.

The microscope was isolated by means of several cushions in the middle of a room in such a way that only vibrations from the piano strings affecting the air and reflected directly towards the open space between slide and cover glass, which was occupied by the organ of Corti and its supernatant fluid, could noticeably affect the hairs — probably by direct transmission from the air to the liquid, since undulatory and other disturbances of the atmosphere are much more readily given up to or transferred from a gas to liquids than to solids. And since the thinner of the two glass plates was supported by wax feet resting upon the other, the motion of both would by this means be more or less damped.

The motion, at any rate, could arrive only by transfer from the

air and not from the vibrations of the solid body of the microscope transferred from the piano through the floor.

It was found that vibrations of the intensity of loud notes on the piano were only with difficulty transferred to the liquid medium on the slide and to the hairs of the cochlea. They were, however, transferred in sufficient degree to set in motion the hairs while not affecting the basilar membrane fibres. Reissner's membrane also accompanied the hair band in vibration, as might have been expected, but in these experiments was present only as loose filaments floating on the liquid.

The vibrations were immensely increased by placing the stand of the microscope on the framework of the piano; in fact, so great was the degree of motion that the hair band disappeared from focus as a body, leaving a faint haze to indicate its presence. Just as the vibrations of a steel rod fixed at one end, when set in rapid motion, are not individually distinguishable, and the rod itself not visible, but appear blended into a hazy band or fan-shaped body, so when the hairs vibrate to a tone, as C', the agitation is so powerful and the oscillation so rapid that the hairs are not visible and the individual excursions not distinguishable. As the tone is allowed to die out, the haze disappears more and more, and finally the hairs return to rest and focus.

That the hairs of the band vibrate individually we are assured by repeated experiment, but that they are differential in their responsive action to various wave lengths or periods we have not been able to satisfy ourselves by direct observation; but we doubt that such is the case, for reasons to be presented later. This much may be said, however: the hairs of the middle and outer end of the hair band are longer than those of the lower end, and the shortest hairs are in the end sections, so that theoretically we would expect the end sections, both proximal and distal, to respond to the higher notes, on the assumption that there is a differential action in the cochlear hair band regarded as a purely physical body, while the centre of the mid-region would be responsive to the lowest notes, grading off towards the higher in both directions. When we remember that high notes are much more valuable to the animal economy than the low ones, and that the tones of the middle group of the commonly used musical sounds are the most powerful in their effect (not the

most intense, penetrating, or irritating) on the nervous system, we recognize that the old idea of a gradual ascent from the lower to the higher notes, or *vice versa*, as the case might be, is probably incorrect, for it would give as much prominence to the low notes as to the high; in fact, the relation of the different tone-perceptive structures was supposed to be very like the relation of the keys of a piano. If, however, the length of the auditory hair determines the selection of the stimulus to be transmitted, then, as it is certainly an anatomical fact that the length of the hairs of the organ of Corti vary from the middle towards both ends, — growing shorter each way, — it follows that it must be a physiological fact that the waves productive of the lowest audible sound affect the hairs of the centre of the organ, while those affecting the hairs of the two ends of the organ of Corti as surely are the highest audible tones, the intermediate portions of the organ being affected by the audible intermediate tones. Thus we find an explanation in the anatomy of the ear for the long-known but never explained or understood fact that the lower end of the tone series falls off very rapidly in the distinctness and separateness of its audible tones (because it has only one-half as many perceptive structures for its lowest tones), while the higher end of the tone series disappears much more slowly for a similar reason.

The vibrations are taken up from the fluid by the free ends of the auditory hairs, and transmitted in the form of undulations to the basal plate of the hair cells; but since I have shown the basal plate to be not a homogeneous structure, but merely a perforated cell end wall, there is no break in the continuity of the undulatory motion, but only a transformation of the form of the wave, *i.e.* a reduction in the extent of the excursion, with the consequent result of an increase in the energy of the undulations transmitted through the perforations of the end plate and the cell protoplasm, to the, and perhaps through the, nucleus, to the nerve ends at the base of the cell. It is not likely that the hair fibrilli are changed in their progress through the nucleus. The undulations are passed down the hairs in several ways, the most common and perhaps powerful being as waves, causing the hairs to bend in a plane perpendicular to the surface of the organ of Corti, at the point of insertion of the hair cells. There are

other means of introducing the undulations to the cochlear duct — among which the diagonal penetration through Reissner's membrane and the penetration through the round window are the most important.

The height of the undulations of the hairs is directly proportional to the intensity of the disturbance in the endolymph. The undulations equal in number the impulses of the endolymph.

The action of the intracellular fibrilli is probably intermediate between that of the hairs and of the nerve fibres; in other words, they serve to transform the physical undulations of the hairs into the physiological stimulation of the nerve fibrils. The nerve fibrils which enter into connection with the cells are, as is well known, non-medullated, varicose, and in some cases apparently branched at their ends. The branching, however, I do not consider to be of special or great physiological importance. The normal, *i.e.* most common, mode of the nerve end in connection with the cell seems to be the fusion of the nerve fibril with the base of the cell, though the point of fusion often appears to be placed high up on the side of the cell. Such a transposition does not indicate that the fibre has entered the cell on its lateral surface, as originally situated, but merely that, in the process of the conversion of the papilla basilaris into the cochlear organ, the cell has been distorted or changed in shape to accommodate itself to its new surroundings, and that its base is no longer directed squarely towards the basement membrane, but at a greater or less angle to it. The inner or outer face, as the case may be, in consequence, becomes in part the base of the cell, but the nerve fibre retains its primitive connection with the cell.

When once the stimulus has been transmitted to the endolymph, the propagation through this fluid produces a concomitant propagation of the undulatory motion along the hair band as a whole, just as a wind blowing across the free and open prairie or a field of standing grain produces undulatory movements of the surface as a whole. A considerable portion of this undulatory motion is taken up by the individual stalks in the case of the grass and by the individual hairs in the case of the cochlea, and is transmitted to the fixed end of the slender structure. Now since physical analogies compel us to assume that all

the hairs cannot have the same dimensions — length,[1] the same relations of reduction in size to the length of the filament and identical basal relations — it necessarily follows that the hairs, like the stalks of grass, will be affected differently by the same vibrational energy, and that consequently many, or perhaps under powerful stimuli all, of the hairs will be affected sequentially by the same impulse, though the stimulation of the nerve ends of different cells, and perhaps of any single cell, would necessarily be different; for our argument it matters not whether the stimulus be a simple, powerful pendular vibration or a composition of pendular vibrations. In the former case, the simple pendular vibration would cause a simple undulation to flow over the surface of the hair band of the cochlea with a regular, even flow, so that the single hairs in transverse groups would be successively affected, and thereby produce a continuous flow of stimulation toward the brain centres, giving rise to concomitant stimulations of the central end organs.

The hairs, however, would not act or react all alike; for the shorter ones, being struck down by the wave motion, would react more quickly than the longer ones, and would consequently not send the same kind of impulse through their end cell, and hence not produce the same nervous disturbance or irritation in the brain as would be produced by the long hairs. This process would be repeated for every segment of the cochlear organ. In the latter case, the hairs would send stimuli of still greater differences, owing to the increased inequality of motion transmitted to the individual hairs.

Since we have found that the cochlear organ is divisible into a series of sense-organ units, we are compelled by all organic analogies to assume that there is at least some small physiological differentiation among the organs.

At any rate, beginning at the base of the cochlear tube and progressing toward the summit, we would have a sequence of stimuli sent into the brain from the sense organ, beginning at No. 1 and progressing to No. 125 (taking a medium number for convenience' sake); and since the nerves of the sense organ, from No. 1 to No. 125, are successively longer, and since the

[1] We know that in different parts of the cochlea they have different lengths, but it is also probable that the hairs borne by a single cell vary in size and length (compare Fig. 9, Plate VIII).

time of propagation of the stimulus, from No. 1 to No. 125, increases the difference of time of the reception of the stimulations in the central end organ, we recognize that there are two sources of variation of the stimulative process of the external or surface organs which must make a great impression on the central end organs, and lend themselves to the formation of suitable associative and co-ordinative processes or the processes of judgment, especially to the recognition of time differences between the stimuli applied.[1] It follows from this that one and the same pendular vibration will send a *series* of stimuli to the brain, and that the stimuli from one source are not necessarily of the same kind; but in all cases the sequence will be the same and the variations the same for any given undulation or series of undulations.

As I have already shown, the hairs end not in identical manner on the top of each cell, and as physical measurements, which I have carried out with all the care possible for the purpose of excluding sources of error, proves the hairs are not of the same size at their basal ends, nor have they the same lineal dimensions. The end cells vary somewhat in size, length, and in the relative position of the nucleus and the manner in which the nerve fibre enters the cell.

Now, these with other frequent modifications of the typical hair cells, or, better expressed, these ever-increasing individualities of the structural relation of the cells comprising the hair band, necessitate the conclusion that each hair cell is somewhat individual in its physiological processes. For example, a cell with long capillo-nuclear filaments will be affected most powerfully by wave motions transmitted to them in time and form, most easily propagated through their substance, and this selection process, having been already applied by the hair itself to the undulation that swept down the hair plate, results in a still finer physical selection, which must still further be modified as it is transferred from the capillo-nuclear filaments to the nucleus, and from the nucleus transmitted through the nucleo-neural filament to the extra-cellular nerve. The modification of the stimulus, during its passage from the nerve through the cochlear

[1] The most essential quality of music rests on the perception of time differences according to some accepted law, to the recognition of which and acquiescence in, the individual lends himself or is structurally inclined.

ganglion cells and the long (relatively) stretch of nerve fibre between the ganglion and the brain nuclei, are, of course, still unknown to us.

Enough has been said, I think, to show that the processes of selection and of propagation of undulations of different wave lengths is an extremely difficult one to follow out in all its detail, and that, although we have gained some new insight into the methods of cell action, the field is practically untouched experimentally and lies before the modern advanced physiologist, an inviting and very promising field for research in neuro-sensory physiology, holding, in fact, the same place in physiology of neuro-sensory processes that the nerve and striated muscle preparations do to neuro-motor physiology, — all of this because of the easily (relatively) controllable physical basis of the sensory processes; the physical basis of smell and sight being so much more difficult of measurement as to practically exclude the acquisition of quantitative results from experimental research in their fields.

From the physical constitution of the cochlea and from the experiments on the hair band it follows that the action of undulatory stimuli in the cochlea leads to very different results from those taught by the Hensen-Helmholtz school (p. 263 *et seq.*). It is certain that only those wave motions are effective in the stimulation of the nerve end organ which succeed in passing all barriers and enter and are propagated in the cochlear canal as discrete wave motions of the endolymph, causing undulations of all the auditory hairs. Any sounding body which gives forth a simple tone as a fundamental accompanied by other simple tones, as overtones, etc., must produce for each tone propagated through the ear to the brain, a discrete series of undulation, which of its own energy stimulates the hairs of the cochlea, and all of them in greater or less degree. It does so in its period entirely independent of the other tones in process of propagation down the cochlear apparatus. A musical or tonal effect produced as Helmholtz conceived in his "compound wave," requiring an analysis by the hair band, does not occur in nature, unless the term "compound wave" is used to designate a group of discrete stresses, any one of which might go on and produce its effect, though all the rest were annihilated. If this is the interpretation of the term, the use of the word

"analysis" in connection with it is not only useless but misleading, since there can be no analysis of the discrete waves when each produces its own effect, no matter what has gone before or is to succeed it. That this term "compound wave" is generally understood in a different sense, the following quotation from Foster clearly proves.

Foster (1891, 92) says on this subject (*loc. cit.* p. 1211): "The vibrations of a musical sound as they pass through the air or other medium are not discrete; the vibrations corresponding to the fundamental tone and overtones do not travel as so many separate waves; they all together form one complex disturbance of the medium; and it is as one composite wave that sound falls on the membrana tympani, and passing through the auditory meatus, breaks on the terminations of the auditory nerve. And when two or more musical sounds are heard at the same time, the same fusion of the waves occurs. Since we can distinguish several tones reaching our ear at the same time, it is clear that *we must possess in our minds or in our ears* [italics mine] some means of analyzing these composite waves of sound which fall on our acoustic organs, and of sorting out their constituent vibrations." Our author, then, continues with an explanation of how the strings of a piano analyze the compound note of the human voice into its component simple tones, saying, "The note sung reaches the strings as a *complex wave* [italics mine], but these strings are able to analyze the wave into its constituent vibrations, each string taking up those vibrations, and those vibrations only, which belong to the tone given forth by itself when struck." The following opinion is equally decisive of the sense of the term analysis as used by physiologists: "The cochlea of the ear resembles a series of differentially toned resonators, an analyzing apparatus which works in strict accordance with Fourier's law, and practically solves the problem in this simple manner. The organ of 440 vibrations selects the fundamental tone, that of 440 × 2 the first harmonic, that of 440 × 3 the second, and so on. Further, each sympathetic apparatus vibrates with an intensity corresponding with the intensity of the harmonics of the note produced; and in this manner the whole note is analyzed into a number of simple tones, in a manner as perfect as any we can conceive.

"After this process of analysis, however, there follows a

process of combination, which takes place in other organs. The fundamental tone, and each of the harmonics severally, irritate a distinct nerve fibre, and each nerve fibre transmits its irritation separately to the brain. Here, however, where the mysterious processes of sensation take place, the several sensations are, in an equally incomprehensible (*sic*) manner, combined into a general one, which gives rise to the sensation of a compound tone. Our perception, therefore, of tones of different pitch is produced entirely by an irritation of different fibres of the auditory nerve. Through the auditory nerve the brain receives from different fibres an intimation of tones of different pitch, which intimation enables it to distinguish the sympathetic vibratory organs which have answered to the tone."

It does not follow that because one is able under certain conditions, as by the use of resonators, careful attention, and selected experiments, to hear overtones and audibly prove their presence in company with a fundamental, that such an overtone modifies the quality of the fundamental tone unless it is strong enough to produce a discrete set of undulations in the hair band, and all undulations of the air, whether they are overtones or not, unless they are strong enough to call forth such discrete undulations and succeed in reaching the hair band, are not perceived and do not help to make the "timbre" of sounds.

Should we construct a series of "pure tone" tuning-forks, vibrating from 15 to 40,000 times per second, having a separate fork for each one-eighth of a tone difference, — on setting these forks in vibration one after another, we should find, providing our ears were properly educated, that we experienced a distinct sensation, which we call a simple tone, owing to the constant difference between the periods and intensities of the pendular vibrations thus set up. It will be, for the present at least, allowable to assume that the proportions of the aërial stresses will be maintained in the endolymph, no matter how much the periods and intensities are modified during transmission to the hairs of the nerve end cells. We should thus have a series of tones ranging from 1 to x. Confining our attention to the cochlear hair cell rows, we are led to look for the physical cause — the sensation of tone (or sound) — in the periodicity, and not in the wave length, as in the case of light waves. One of Koenig's experiments illustrates this very well. Two simple forks are

set in vibration, one having 512 vibrations per second, and the other 100 vibrations per second. Each of these periods is recognized by the brain, as near as we can measure simultaneously, as a distinct tone. Without, however, introducing any other vibrating body into the experiment, we may, under proper conditions, hear two other sounds, one of which we recognize as a tone, the other as a sound. These two sounds are due to the production of maxima and minima of stress, by the presence of the two series of vibrations of periodicity 512 and 100 respectively, journeying in the same direction through the air, but with unequal steps. The tone is the same as that produced by a fork having 88 vibrations per second, and the sound the same as one having only 12 vibrations per second; and it is found that these two sounds are produced by "beats" in the two streams of sonorous vibrations.

The ear may thus recognize at one time three distinct tones, propagated through the same mass of air and endolymph. This individual perception may be due to the presence in the hair band of filaments which respond only to special wave lengths; it may be due to the successive response of all the hairs to all the varying stresses of the uneven stream, as illustrated by a wheat-field in a gusty wind; or it may be due to a combination of both these factors; and to the latter view I incline, giving preponderance to the second condition.

Analysis of sound (or sound waves) is then, according to my conception of the auditory function, a process which does not occur in the way in which it has been previously supposed to take place. From a study as complete as we can yet make it, the auditive process is seen to be so different from the Helmholtz-Hensen conception that the use of the word *analysis* is not admissible. There is in reality never an *analysis*, either in the end organ or in the central apparatus; but each external physical variation that succeeds in producing an alteration of the end organ (practically superficial, *i.e.* lying on the bounds between the mass of the sentient matter and the external) is *propagated* simply, it may be in more or less converted form, but still a direct and continuous transmission of a variation of previous relations of external matter. While journeying in company with other undulations, a sonorous undulation is subject, not only to change, but to annihilation as well. Only after

reception within the cochlea and its transmission to the brain does it become transformed in a manner yet unknown to us, but which we express roughly by the terms association and co-ordination, so as to produce something else than a mere propagation of auditory stimuli. When this stage is reached, we have, instead of an *analysis*, a *synthesis* of stimuli. There is, then, in the auditory processes never analysis, but always, as the final resultant of the always sequential stimulation of the auditory apparatus, a synthesis of auditory stimuli.

It must be admitted on physical grounds alone that vibrational impulses affecting the tympanum may, and under ordinary conditions of the middle ear must, affect the membrana fenestræ rotundæ by transmission across the middle ear, by means of the contained air, and that the impulses so produced in the cochlear organ must either be propagated or destroyed. In this connection I wish to make an addition to the previous conceptions of the processes taking place in the cochlear tubes while undulations are propagating themselves through the contained liquid. It has not, so far as I have been able to discover from the literature, ever been considered that the increase of tension, which has been assumed for the cochlear liquid to take place and to be transferred to successive parts of the liquid during the passage of undulations, could be relieved in any other way than by the bulging out (*i.e.* into the tympanic chamber) of the membrane of the fenestra rotunda. The readiness with which such increased tension could be relieved, through the endolymphatic duct on the one hand, and by the propagation of the undulations through the perilymph from the endolymph on the other hand, has not been in the least recognized, so far as I can learn. The pressure stress in the perilymph is, with the greatest readiness, conducted out of the ear; and since the undulations of the air are so very slow, as compared to those of the liquid (as 1 to 5), that they are readily and successively annihilated before the succeeding stimuli are received, I do not think any sufficient objection can be brought against the view that auditory stimuli may be propagated through both of the fenestræ simultaneously. *It is most certainly true that impulses going through both openings simultaneously are not necessarily antagonistic;* and it is also equally true that, owing to the greater rapidity of transmission of the waves through solids

than through gases, the transmission through the tympano-cochlear chain of bones tends to be more rapid than that through the air to the round window; but it is at the same time counterbalanced somewhat by process of transfer, owing to the lost motion (under certain conditions of the osseous chain), which is a disturbing feature of the process of transmission to the oval window.

There are three phases in the result of the stimulation of the auditory cell: first, the period of preparation occupied in the propagation of the stimulus through the cell protoplasm, *i.e.* through the capillo-nuclear and the nucleo-neural filaments of the nerve end cell; second, the period of excitation during which the filaments are transforming the stimuli received into the nerve stimuli; and, third, the relaxation period occupied in regaining the normal condition of repose and cell activity, during which time the accumulated stimuli have passed over into the nerve and left it as before.

In dealing with the *differences of sounds*, physiologists are generally agreed that there are three distinct conditions inherent in the *physical* constitution of sounds which give them their individuality. They are the *intensity*, the *pitch*, and the *timbre*.

The intensity or force of sound depends upon the amplitude of vibration of the sound wave, and there can be no doubt that this is strictly a differential quality inherent in the physical basis alone.

The pitch of a sound depends upon the number of whole vibrations (complete aërial undulations alone referred to) executed by the auditory wave in a given period of time, as Mersenne discovered in 1636. This, also, is easily proven to be a differential quality of sound entirely dependent upon the physical condition of the aërial undulation.

The quality, *klangfarbe*, or timbre of sound, depends, according to Helmholtz, upon the *form* of the *sound wave* as caused by either the *quality* or *form* of the sounding body; such quality or form of the sounding body influencing the timbre of the produced sound by varying the number, pitch, and intensity of the subdivisional tones and harmonies.

This so-called third property or individual quality of sounds cannot be shown to be due to a third physical condition of the aërial undulations; on the contrary, it is caused by action of the

two qualities already considered, and to them alone, acting upon or conditioning numerous secondary vibrations which always accompany musical sounds, especially those produced by ordinary means. It is also true that the *klangfarbe* is due more to education than to anything else, for to ordinary ears the finer qualities of *klangfarbe* are unperceived.

Consequently the tonal differentiation which has been previously referred to the *klangfarbe* as form of the acoustic wave must be referred to the two primary and only modifying influences. Timbre is due to the sequential propagation of the same (or nearly the same) accented series of sonorous undulations up the cochlear hair band. The accent may occur either before or after the arrival of the other member; *i.e.* the recurrence of the series may be marked by the accent or fundamental tone, or the latter may occur in any part of the series, provided it recurs in the same (or nearly the same) relative position with reference to the other tones.

Ordinarily these tones follow each other with a rapidity, when their faintness is considered, which prevents their being recognized as separate tones, but this is by no means always the case; for some of the partial and harmonic tones accompanying the fundamental note, *e.g.* of a piano string, are readily distinguishable as independent tones when *attention* is paid to them alone. It is also true that other tones of the harmonic series stand in the same relation to the main partials that these occupy with reference to the fundamental.

It should be borne in mind that the perception of sound by the ear does not follow with mathematical accuracy the laws of physical acoustics.

The *rhythm of intensities* is, then, the cause of the *timbre of tones*. We may illustrate in a crude way how the same nerve fibres may send sequential stimuli of different intensities, and give rise by increase of rate into blended sensations.

Suppose we fill a sufficiently long glass tube of small calibre with liquids of sweet, sour, bitter taste in the order given, each taste occupying a few millimetres' length of the tube and strong enough to give rise to the special sensation, yet weak, evanescent enough not to fatigue the nerve or persist in the tongue to the detriment of the experiment. Starting slowly, cause the liquid to flow in a stream over the tongue, and there will follow suc-

cessively sensations of sweet, sour, bitter, at a rate corresponding with the length of the section of each taste in the tube and the rapidity of the flow. By increasing the rapidity of the flow, the sensations become less distinct and finally blend into a mixed sensation of bitter sweet, sweet sour, or any of the other possible combinations of these flavors, depending upon the relative predominence of any single one of the liquids. But the nerves of taste do not analyze this compound sensation. It is analyzed in the brain, but even there only on the basis of education as to what constitutes the peculiarities of the sweet, sour, and bitter taste used.

The same character of experiment may be tried, with about the same results, in the case of the nose, except gases are preferable to liquids.

Or, again, the sense of touch may be experimented upon in a similar manner by causing an endless rod whose succeeding sections of a few millimetres in length are alternately cool and warm, to pass over any temperature-sensitive surface of the body. The sequence of varying temperatures may have any arrangement desired, and the result is not essentially altered. The sensations, when following each other with a rate sufficiently slow, are transmitted individually to the brain by the same nerves; but when the rate is increased beyond a certain limit, they become more or less blended into a single temperature sensation. There is no analysis of the sensations here either in the end organ or in the brain, unless previous experience enables the person to determine, on general grounds, that the sensation is produced by a sequence of stimuli of varying temperatures. Again, the eye and the brain fail to analyze the sensation due to a rapid succession of colors into the component colors. And yet a *mental* analysis is possible on the basis of previous experience and education in the composition of colors.

After explaining at length his view that the quality of a tone is due to the *form* of the sound wave (*loc. cit.* Chap. I, "Form of Sound Wave"), Helmholtz comes to the consideration of "Apprehension of Qualities of Tone," Chap. VI, p. 119, and concludes from a series of experiments that "the quality of the musical portion of a compound tone depends solely on the number and relative strength of its partial simple tones, and in no respect on their differences of phase." Or, in other words, the

timbre of a tone is due to the sequence of certain simple tones, and not on the form of the wave compounded of them.

Or, as Bernstein states it, "the sensation of a note is caused by the irritation of a certain fibre of the nerve of the cochlea, which is produced by the fundamental tone, and also by the more or less feeble irritation of certain other nerve fibres, the terminal organs of which have been irritated by the harmonics." On the supposition, of course, that each hair cell received from its supporting basilar membrane fibres stimuli due to a given frequency.

Koenig has, I think, conclusively proven that *timbre* is due to the presence of what he calls the sounds of subdivision (Helmholtz's "oberpartialtöne," translated by Tyndall into "overtones"), which are not identical with the "harmonics." These subdivisional sounds are produced by *non*-periodic as well as periodic waves, and hence the quality, pleasing or otherwise, of the tone may be due to non-periodic undulations as well as the periodic, to which alone Helmholtz restricted them. Helmholtz was led by experimental results to hold the view that *timbre* was due to the *form* of the sonorous wave, and that in the succession of upper and lower partial tones or tones of subdivision, the form of these wavelets must necessarily remain constant. Koenig has shown that Helmholtz's error lay primarily in the apparatus which he used, and that as a fact, *although the form of the wavelets is constantly changing, the ear nevertheless does under normal conditions "group the result as a unitary sensation."* These experiments of Koenig's prove the correctness of the view I had already arrived at; viz. that there are in reality but two conditioning physical relations of the tone wave, — its rapidity and its kinetic energy.

The sound wave, strictly speaking, has no form; it is not a discrete thing, but only a condition of the matter gaseous, liquid, or solid, which in all cases partakes in the physical basis of sound. And from the external vibrating body to the nerve end cell the vibration is transmitted without assuming form: such, at least, is true of all the acoustic undulations which produce the sensation of sound in the brain of man. It is demonstrable, as Helmholtz claims, that two notes of the same pitch and intensity, but from different sources (*e.g.* middle C from the piano and violin) reaching the ear simultaneously, do not

strike upon the tympanum as two distinct impacts so far as their fundamental tones are concerned, but as single condensations and rarefactions or pressures and relaxations as the motion is transferred mechanically from the air to the ear drum. This main (combinational) pressure and relaxation is accompanied by minor ones of different pitches and varying, but in all cases less, intensities. When these are further transmitted and produce the sensations of tone, how does the ear separate the subdivisional tones and harmonics of the piano note from those of the violin note? As Koenig has clearly shown, "if the ear could always separate the pure *harmonic* or absolutely *inharmonic* partials from their fundamental tone, or if it always heard pure harmonics as an indistinguishable part of the unity of the timbre of a fundamental tone, then we might draw a hard and fast line between mere mixtures of sound and timbre." Such, however, is not the case. We cannot perceive these minute distinctions without special care and physical aid; for often the ear cannot detect the inharmonious partials when present, and does, on the other hand, often separate out the harmonious partials (Koenig), and, besides, in the last analysis, timbre is simply due to a rapid accented sequence of tones, and not to a *mixing* of simple tones.

Here, as elsewhere, however, much depends upon the sensitiveness and delicacy of the ear and central association apparatus. The passage of sound through the ear of one person is much the same as the passage of light through a plate of glass, while in the ear of another (or perhaps the brain) the same apparently simple unitary sound would be drawn out in a harmonious chord much as white light is separated into its spectrum of component colors by passing through a prism. Koenig concludes from his experiments that melody is associative rather than physical.

That the appreciation of sound is a mental act has long been recognized, and Foster cautions us to bear it in mind. This being true, and allowing for the moment that there is an analysis of the compound sound wave by the fibres of the basilar membrane, or any other auditory structure, Foster does not make clear how this can be so, while at the same time, as he says (*loc. cit.* p. 1214), "We do not receive a distinct series of specific auditory impulses resulting in a specific sensation for every

possible variation in wave length of sonorous vibrations, any more than we receive a distinct series of specific visual impulses for every possible wave length of luminous vibrations. In each case we probably have a number of primary sensations from the various mingling of which, in different proportions, our varied complex sensations arise; the difference between the eye and the ear being that whereas in the former the number of the primary sensations appears to be limited to three or at least six, in the latter, thanks to the organ of Corti, the number is very large: what the exact number is we cannot at present tell." There could be no genuine analysis unless the ear did in some way respond to each vibration in wave length, and from the anatomy of the cochlear sense organs this is very probably the case. The manner in which this is carried out has already been indicated.

There is, however, on further consideration, another set of conditions which probably affect the appreciation of sound; viz. the state of the sensorium into which the sound waves enter. This state is determined by previous and present sensations not from the ear alone, but from other sense organs as well, and is sufficient to determine the ultimate sensation due to a given stimulation by sound waves. This is, however, a subject of great obscurity and difficulty, but it should not be left unconsidered in any discussion of the qualities and conditions of psychical audition. These phenomena belong to the still unknown borderland between the external tone-generating physical universe and the internal psycho-physiological tone-perceiving apparatus, — the auditory hair and ganglion cells of the auditory centres with their numerous connections with other apparatuses of the brain. There is a gradation of phonomena from the purely physical and external to the purely subjective or internal auditory sensations. The latter are not primarily dependent upon the former, and include phenomena of subjective music by mental effort and all involuntary subjective tone perceptions. As an example of the latter class of phenomena I give the following personal experience. I had been riding all night on the cars and was engaged in reading the morning paper, and as I sat but a few seats from the car door and facing it, I could hear distinctly the slamming of the door as trainmen passed in and out. As I had lost the night's rest, the quiet

attention to my newspaper favored my dozing into semiconsciousness, from which I was suddenly startled by what at first seemed to be a sharp blow upon the newspaper in front of me, but before I could open my eyes I was perfectly conscious that this was an illusion, and that the paper had not been struck and had not given forth the sound. This was confirmed by seeing the conductor coming from near the door, which he had just slammed, and by finding my paper in its former position. Now the sense organs whose *attention* had been last directed to the outer world were the eyes, and the stimulus entering the brain through the ears was referred to their field of vision, but the stimulation of the auditory centre had been so keen that the distinctive qualities of the sound of a slamming door at once corrected the illusion that it was the paper which had given forth the sound, notwithstanding the fact that the first impression had all the distinctive qualities of a sharp blow upon the paper. In this instance the *timbre* or tonal qualitatives distinctive of the slamming door were for the instant suppressed by the state of the co-ordinating mechanism, though they were soon recognized. We have to go but a step further to recognize that such internal modifications may become permanent.

The auditory perceptions are largely dependent upon education. This is true of the results of all sound stimuli; thus, in the young child possessing auditory organs structurally perfected, as far as the microscope reveals, we find a great lack of the "proper" appreciation of sounds and tonal compositions, — a lack due to small experience, *i.e.* to a lack of co-ordinating powers in the central nervous system. We depend for our judgments of the direction on the constant relation maintained between the external ear and the auditory meatus to the surrounding air, and we are very liable to false judgments on any alteration of the normal relation. If, for instance, the hand or other solid body be placed close to the side of the head and in front of the ear, the entrance of sound waves is modified much as it would be were the external ear to be revolved about the meatus as an axis, and hence the sound waves make their way in from behind with greater facility than from in front.

We are greatly assisted in recognizing the direction of sound by the position of the external ear on the side of the head, since it renders the perceptions of sounds of like intensity

easier from in front than from behind, from below than from above; and this condition being ever present, the co-ordinating mechanism is adjusted to it, and thus our judgment of direction is rendered easier and more frequently correct than it would otherwise be. Sound is heard most distinctly when the auditory canal is in the same straight line with the direction of the sound waves, and for this reason we turn the head in various directions in order to ascertain the position in which the sound seems the loudest; and the line passing through the centres of both ears will lie in the plane in which the most intense sound waves are propagated. This plane is of necessity at right angles to antero-posterior or sagittal plane or plane of direct vision. All judgments involving the use of the auditory apparatus for determining direction and relations of external bodies must necessarily start from this fundamental relation, which is so early recognized as to be during adult life passed over unnoticed. In the position of the ear above referred to one ear receives the greatest possible, the opposite ear the least possible, amount of sound, and the appreciation of this difference, *i.e.* the determination of the position of the head in which the greatest difference exists, is used directly in determining the direction of sound, the judgment being based upon a comparison of the intensities of stimuli. The necessity for making trial attempts in order to establish the position of a sounding body by the ear has been compared to the execution of movements in binocular vision, by means of which we estimate distance, determine direction, etc. The assistance gained from the eyes in determining direction in such a case is not slight, but is usually an unconscious effort, mainly unnoticed because there is a continued effort maintained by the nervous system for the proper orientation of the body in space such as is necessary for its perfect control. All sensations whatsoever going to the brain from the surface of the body likewise aid materially in its orientation.

Although the ordinary method of transmission is through the air, liquid and solid substances prove even better conductors when brought in contact with the hard parts of the head. When the head is immersed in water, all sounds that are transmitted to the water pass with increased facility and intensity to the internal ear, in part through the bones of the head direct, but also in part through the mediation of the tympanic membrane

with the cushion of air inclosed between it and the water, which may enter only part way into the meatus auditorius externus and incompletely fill it. The inflow of many of the constant stimuli from without being prevented, the transmission of internal vibrations arising from the cardiac pulsations and the rush of blood through the blood-vessels, the rustling sounds due to the passage of air currents through the pulmonary passages and other respiratory ways, being greatly increased, one is able to hear with remarkable distinctness the great amount of noise of several kinds which these physical processes make.

The very remarkable noise produced, for example, by the contraction of the temporal and masseter muscles resembles very closely the incessant clatter of a large number of telegraphic instruments being operated simultaneously. There is a distinctive character possessed by these sounds, due entirely, I believe, to the greater intensity of the vibrations of liquid and solid media over those of gases.

It is said that the transmission of vibrations by means of the bones of the skull is of no importance to animals above the fishes, but that in these (possessing no external ear) the head bones play a very important part in the transmission of sound; in fact, it is about the only means for the transfer of the sound waves. This is certainly true, so far as concerns the main uses to which the human ear is put, but we cannot doubt that the ear plays an important part in keeping the internal organs in normal condition of work by sending in a continuous stream of stimuli due to pulsations of the circulation, respiration, and all of the many processes which cause vibrations either in the lymph channels or the bone about the ear. The musical sense as it exists among civilized and cultivated races is a result of the association of ideas and of tone production, and not of a perfection in the apparatus for tone perception in the ear.

G. RECAPITULATION OF SOME OF THE TOPICS, WITH A FURTHER CONSIDERATION OF A FEW OTHERS.

Recapitulation B.

1. Since the beginning of this century the idea that the lateral line of fishes was related in some way to the higher sense organs, nose, ear, and eye, one or all of them, has never been absent from the minds of morphologists; and although, when first expressed, the lateral line was considered to be merely a series of mucous pockets more or less completely joined into a canal without even a suspicion that they had nervous attachments or contained sense organs, still it was believed and categorically stated that since these structures were in line on the side of the body with the higher sense organs on the head, and since they found their place between the dorsal and ventral groups of trunk muscles, they were in all probability related to the higher sense organs. Some authors thought that they were the parental forms; others that they were derivatives of ancestral organs which were the parental type; others, again, homologized the "mucous pockets" and canals of the lateral line with the tracheal canals and stigmata of insects, which were then quite generally believed to be auditory in function, and they claimed that the vertebrate ear was the greatly modified product of a mucous pocket which had somehow or other acquired the sensory structures and their accompanying nerves.

This idea has grown in strength in successive generations with each renewed investigation, until now, confining ourselves to the ear, it may be said to be fully established. The investigations of Leydig in demonstrating the nerve supply of the contained sense organs in these canals, or rather in their "mucous pockets," opened the way for the score or more of workers who have increased our knowledge, and among whom we find the names of Leydig, Ball, Bodenstein, Schulze, Solger, Emory, Dercum, Fritsch, and Allis, some dealing with the morphological data alone, others with the physiological side as well. The one point of general agreement among all has been the great resemblance of the canal sense organs to the maculæ

and cristæ acusticæ of the ear. The deep-seated existence of this belief is very impressively illustrated by the fact that when new facts have been discovered in the anatomy of the ear organs they have been found to be true of the canal organs, and *vice versa*. Likewise, the errors in our knowledge were common to both. The ontogeny of the ear has disclosed many new facts, and as fast as the ontogeny of the canal organs has been worked out they have been found to agree in the details of their ontogeny with the ear canal organs no less than in their adult anatomy.

The processes which I have described in the chapter dealing with the development of the ear canal complex were not known to occur in the development of the lateral line canals, and von Noorden's circumstantial account of the formation of the cristæ acusticæ and their ampullæ and canals remained, like all previous accounts of ear anatomy and development, a series of dry facts, until leavened by the addition of Allis's germinal series of facts concerning the development of the surface sense organs and their canals. Then the slumbering idea, already a century old, arose in a concrete demonstrable form and became clothed in a garment of facts logically arranged and consequently easily grasped and understood. Indeed, so easily grasped, that already, before all the details are worked out, we have forgotten that there was any difficulty or uncertainty about the demonstration of the old, half-perceived idea, which was so uncertain in form that men were not quite sure that all this homology might not be mere parallelism.

2. In describing the Elasmobranch ear I have emphasized the necessity of keeping in mind the relation of the chambers and channels of the internal ear to each other as that of a complexus of surface sense organ canals sunk below the surface of the head with the dermal surface (from which the canals are generated), as the lining of the main chambers — the two coordinate and primary chambers of the ear. It was found that in Dasyatis the ear presents a remarkably symmetrical arrangement of parts which, taken as a typical form, permits of the union of *all vertebrates* according to a simple and logical plan of development (so far as the ear is concerned), and satisfies as well all the demands yet made by any anatomical facts, for the derivation of the ear from pre-existing surface canal organs.

3. It is proven that there is no essential difference between the sense organs of the internal ear of the vertebrate group and the superficial sense organs of the Ichthyopsida as they exist in the surface canals of these forms. Both consist of canals containing sense organs lying below the surface of the body, and they may (as in ordinary canals and the ear in some Elasmobranchs) or they may not (as in Savi's vesicles and the ear in the majority of vertebrates) communicate with the surface. Both forms may or may not be entirely inclosed in cartilage or in bone.

4. The *semicircular canals* of the ear are simply remnants of the canal system of the surface, and although bent into shapes more or less semicircular, they still retain their communication with the (morphological) exterior by means of their terminal (*i.e.* surface) pores or openings in the walls of the utriculo-sacculus, which in its turn often communicates with the surface of the head by the endolymphatic duct or surface canal.

5. The sense organs of the ampullæ not infrequently divide without causing the division of the canal, and even the crista abortiva in some Elasmobranchs and Reptilia has divided, each sense organ resulting being supplied with a distinct nerve branch. The fact of the presence of two parts in his so-called macula neglecta was not understood by Retzius, who first observed it.

6. When the division of the sense organ has proceeded so far as to cause a separation of the previously unified nerve trunk supplying it, we are justified in concluding that the number of sense organs in the group is at least equal to the number of discrete nerve twigs supplied to the group.

7. Each offspring resulting from the division of a canal organ inherits a tendency to division and canal production. The auditory canal sense organs of the second generation divide symmetrically when considered in their mutual relations, but individually the division is an asymmetrical one. The third generation shows the same characteristics.

8. Thus it is true that the development of the semicircular canals in the ear is due to phylogenetic and mechanical causes, and is not in the least a response to physiological necessities or requirements, and conversely the canals have no active part in the auditory function. They serve merely as chambers to hold the liquid necessary to float the auditory sensory hairs.

9. The Cyclostomes and some Elasmobranchs possess two endolymphatic ducts, or surface canals, on each side of the head, one of which on either side bears a canal sense organ supplied, so far as our anatomical knowledge reaches, by the facial nerve, or more exactly by the so-called auditory accessory nerve, which is said to be a branch of the facial. In this connection Mayser's conclusions as to the relation of all canal organ nerves to the auditory proper should be borne in mind.

10. The otoliths in the ear chambers are to be considered as essentially foreign bodies which are tolerated because of the impossibility of getting rid of them. They are the result of the secretive action of the ectoderm cells, which in ancestral forms produced the surface scales. The higher we rise in the vertebrate series, and also the greater the auditory sensitiveness, the fewer the otoliths found in the ear.

Those sense organs whose condition indicates their predominance in auditory work have no otoliths.

11. It is found that the sense organs of the cochlea undergo a series of transformations heretofore overlooked and that there is an organ in the adult cochlea of the hydrosaurian Reptilia which makes its appearance in the embryonic mammal, but together with its nerve supply fades away before adult life is reached. Whereas the cochlear organ of birds, for all that we know to the contrary at present, seems to be of the form of an undifferentiated plate of sensory cells, in the Alligator and in mammals the organ of Corti becomes differentiated into a linear series of organs or cell groups, which are individually morphologically equivalent to the other simple sense organs of the ear, *e.g.* the cristæ acusticæ. This segmentation of the organ of Corti is indicated by (*a*) the hair cells, (*b*) the supporting cells, (*c*) the blood-vessels, (*d*) the nerves, and consequently the skeleton (the lamina spiralis ossea) and the soft parts (the membrana basilaris) of the floor, transmitting these last two structures, *c* and *d*.

12. The cells which line the sulcus spiralis internus in the adult are all that are left of the large epithelial ridge of the embryo. This ridge is composed of long columnar cells which grow shorter and disappear. It is not yet ascertained what the mode of disappearance is. It may be that the columnar cells

are entirely absorbed, in which case the lining epithelium would be equivalent to the "Ersatzzellen" of Ketel (in Petromyzon), or it may as well be that the long columnar cells are simply reduced, on account of decreased nutrition, and appear as cubical or spherical cells. No explanation has yet been offered of the apparent fact that there are no small surface hair cells in the Sauropsid organ in the developing mammal such as exist alone as the sensory elements (?) in the hydrosauria. Where are these short cells or what represents them? How many of the long epithelial cells in the embryo mammal bear hairs, and where are the supporting cells at this stage?

13. The so-called membrana tectoria of previous authors is in reality a hair band or field of long slender hairs which spring from the tops of the hair cells and form a waving plume on the crest of the ridge of the organ of Corti. Each hair cell gives off a bundle of about two dozen hairs which spring from the whole surface of the cell cap (Didelphys, Mus, Bos, Sus, Homo), and each individual hair floats freely in the endolymph.

14. The membrana tectoria, the membrana reticularis, Loewenberg's net, and the three or four main trunks of the system of spiral nerves of the cochlea have no existence as such in the living mammalian ear, the first of them being the chemically and physically modified hair band; the second one being an artifact produced by the separation of the cell caps of the organ of Corti from their cells, in the form of a continuous and more or less perforated plate; the third structure being likewise an artifact produced by chemical and physical agents in ever-varying form; while the fourth one of the artifacts mentioned is in all probability the product of the transformation of the walls of a lymph space with adherent and included nerve fibres, cell processes, and cell remnants.

15. The cochlear nerves end *in* the hair cells and *not* freely *between* them, and they are probably continuous with the auditory hairs, as Hasse claimed, and as my own observations render almost certain. The continuity of the hairs with the nerve fibres is established by the protoplasmic ways inside the hair cells, which I have designated the capillo-nuclear and the nucleo-neural filaments. Free nerve ends do not exist in the auditory epithelium, and consequently Helmholtz was entirely wrong in ascribing to the auditory otoliths the function of tetanomotors,

which stimulated the nerves by compressing them or delivering suitable blows on or near the ends of the fibres.

16. The membrana basilaris is far too complex a structure to permit of its use as a vibrating membrane capable of responding in its various parts quite independently to sound stimuli of varying wave lengths.

The membrane is composed of several superposed sheets of fibres and adnexed cell masses, and, as I have recently discovered, there is also a special *vascular layer* (Sus, Bos) or system of basilar capillary loops, which layer is placed between the fibrous layers and for the most part below the nerve fibre layer of the inner border of the membrane. This vascular layer is composed of numerous circuitous capillary channels which have been overlooked by previous investigators. The basilar membrane cannot possibly meet the physical demands made upon it by the Hensen-Helmholtz "piano-string" theory, and, as I have shown, its phylogenetic history proves it to be a modified portion of the skin of the head which forms first and last the floor upon which the sense organs rest.

17. If the ear originated from surface canal organs and their inclosing canals, it became evident that the older view of the segmental value of the so-called VIII or auditory nerve could not be true; if the view of the morphological value of the VIII was indeed true, then the origin of the ear from surface canals could not be true in the sense claimed; consequently this apparently fatal objection must be removed. An examination of the present state of our knowledge of the auditory nerve supply, together with a few additions I have been able to make to the subject of the innervation of the auditory sense organs in the Cyclostomes and Elasmobranchs, proves conclusively that throughout the vertebrate group the same plan of innervation is maintained which is laid down in the Cyclostomes and that a dual peripheral origin and a dual central termination of the auditory nerve fibres in intimate connection with the VII and IX respectively, is the first fundamental fact of ear nerve supply. The ear organs are innervated by the nerves which supply surface canal sense organs. The genetic relationship of the VII and IX nerves to the VIII is shown by the entrance of the parental nerves into the auditory capsule, where they both give off nerve branchlets to supply ear sense organs and then

pass on to the surface of the head, where they again supply canal organs of the lateral line system. The VII enters the auditory chamber and gives off nerves to ear sense organs in forms as high as the saurian Reptilia, and it is possible in the Mammalia as well, though the latter point has not been proven. The IX nerve enters the auditory chamber and gives off a nerve to the sensory apparatus of the ear in Elasmobranch fishes at least.

There has been great difference of opinion as to whether the facial nerve really gave off a branch to the ear in Petromyzon, and the whole matter has been summed up by Julin (1890), who says (p. 819), after showing that all the anatomists who have studied the facial in Petromyzon are agreed that this nerve makes its way into the auditory capsule to traverse it and pass out again from its anterior lower corner: "Pendant son trajet à travers la capsule auditive, le nerf facial fournirait, d'après Schlemm et d'Alton au vestibule membraneux un petit rameau nerveux, qu'ils appellent *nerf auditif accessoire*. Cet fait a ensuite été confirmé par Ketel. Ce rameau du facial a été également mentionné par J. Müller comme existant chez les Myxinoids. Furbringer sans en nier l'existence, n'a pu cependant le découvrir, ni chez *Myxine glutinosa*, ni chez les Petromyzons. Wiedersheim, qui n'a pu non plus en déceler la présence chez Petromyzon, émet l'idée que ce nerf acoustique accessoire de Schlemm et d'Alton ne serait autre chose que le nerf oculomoteur externe (abducens). Enfin, Ahlborn n'a par non plus signalé cette branche du nerf facial. Pas plus que ces auteurs, je n'ai pu en trouver la moindre trace chez l'Ammocœtes." This branch *is present* in the ear, and it is more probable that those authors who have studied this nerve specially and who have followed it through its whole course have described it correctly than that those who have failed to find the nerve have really proven the absence of such a facial branch. We know from Ahlborn's studies that the recurrent branch sends facial fibres into both the glossopharyngeal and the lateral nerves.

According to His, Sr., the auditory nerve is purely a ganglionic nerve, and the same is true of the taste fibres of the IX. As is well known, the sensory fibres subserving the sense of taste in the anterior two-thirds of the tongue run through the chorda tympani, and the recent investigations of Sapolini make

it fairly certain that the chorda tympani is a continuation of at least a portion of the fibres of the portio intermedia Wrisbergi, which pass through the ganglion geniculi to the chorda tympani. It follows from this that the taste nerves of the IX are ganglionic in origin and from the same source as the common acustico-facial trunk (of course by this term I include only the vestibular trunk of the VIII, which properly belongs to the VII. His does not make this distinction). Again, on p. 422 our author says: —

"Der acustico-faciale Ganglioncomplex bildet ursprünglich ein Ganzes und er scheidet sich nicht etwa bloss in zwei hinter einander liegende Segmente, in ein Facialis und ein Acusticusganglien, sondern es entstehen aus ihm vier bis fünf in ihrer Lage eigenthümlich sich verschränkende Theilstücke. Es trennen sich einestheils die intracranialen Würzelganglien ab, welche die Anatomie theilweise noch als Acusticuskerne (nl. acusticus inf. von Henle), accessorischer Kern (von Schwalbe) u.s.w. aufzählt, anderntheils aber scheiden sich Ganglion vestibuli, G. geniculi, und G. cochleæ, von einander, von denen des G. geniculi swischen die beiden Acusticusganglien eingekeilt erscheint. Das dem Facialis besonders zugetheilte Stück kann morphologisch von den beiden Acusticusganglien nicht getrennt werden, so gross auch der physiologische Gegensatz sein mag." As showing the deep significance of Mayser's original statement concerning Teleosts, that the lateral line nerves terminated in the brain in company with the auditory nerve, it is interesting to note that Strong has recently corroborated this fact for another group of the Ichthyopsida, viz. Amphibia.

18. In 1817 Johan Fried. Meckel published a treatise on human anatomy in which he propounded certain views regarding the morphological value of the cranial nerves, which have not received due recognition from anatomists. He says (Bd. III, pp. 668 and 787): —

"Alle Hirnnerven sind einzelne Abtheilungen von Rückenmarksnerven, welche sich nicht wie diese zu einem Stamm vereinigt, sondern zu einzelnen Nerven entwickelt haben, und der Grund dieser Abänderung des ursprünglichen Typus ist theils die Entwickelung der Centralmasse des Nervensystems im Innern des Schädels, sowie des Schädels selbst, wodurch die einzelnen Abtheilung der Nervenwurzeln sowohl bei ihrem

Entstehen als in ihrem Verlauf mechanisch auseinandergerückt werden, theils die Eigenthümlichkeit der Gebilde am Schädel, der Sinnesorgane, deren Wurzeln durch die Nerven, welche sich zu ihnen begeben, gebildet werden und deren Eigenthümlichkeit der Entwickelung eigener Nerven parallel läuft."

"Dass sich wirklich nicht neue Nerven anbilden, sondern nur ganze Nerven zerfallen, einzelne Aeste derselben sich zu ganzen Stämmen erheben und von eigenen Hirntheilen entspringen, ergiebt sich für manche derselben aus der vergleichenden Anatomie unwiederleglich, indem eigene Nerven, namentlich Sinnesnerven höherer Thiere, bei den niedrigen Thieren nur untergeordnete Aeste anderen Nerven namentlich des dreigetheilten sind, dies um somehr, je tiefer das Thier ist." The direction of this differential process is, according to Meckel, a postero-anterior one. He says further: "An den hinteren Nerven spricht sie sich nur durch Nichtvereinigung der hinteren und der vorderen Wurzeln der Nerven aus, *die vorderen dagegen scheinen dadurch zu entstehen, dass sogar einzelne Bündel zu eigenen Nerven sich erheben.*"

Although Meckel stated thus distinctly the principle of structural differentiation of cranial nerves out of *branches* of previous spinal nerves, his classification shows that this generalization was not based on conclusive anatomical proof in the case of any single nerve or group of nerves.

Recapitulation C.

19. As Froriep has shown, the ectodermal thickenings which Beard described as giving rise to the lateral line organs have in fact another fate. The genuine lateral line organs escaped Beard's observation, and in consequence Beard's conclusions as to the homology of the vertebrate auditory organ are incorrect.

20. The detailed comparison of the anatomical characters of the surface sense organs (canal organs) of the existing Ichthyopsida and of the embryonic stages of the Sauropsida and Mammalia as well, fully sustains the conclusion that the ear is only a modified member of this group of sense organs, and that the cupulæ, auditory clubs, and all such structures found in connection with the lateral line organs, are artifacts produced in the main from the auditory hairs of the sensory cells.

21. The above conclusion is rendered certain by my discovery that *in Elasmobranchs the structural connection between the ear organs and the surface canal organs is for a long time maintained* after the ear has migrated to its internal home, and in some forms may be said with truth to persist during the life of the individual.

22. In the Mammalia the anterior and posterior canals, by uniting, fuse their two half-pores into one pore, which maintains the open communication of the semicircular canals with the morphological surface of the head. Thus we have in the human ear involution on involution; for the main chambers of the ear, utriculus, and sacculus, are the result of an involution of a portion of the surface of the head into the tissue below, while the semicircular canals forming later are the result of involutions from this ear surface.

Recapitulation D.

23. The three semicircular canals arise in all cases which have been adequately studied from three depressions, and their upgrowing walls are formed in connection with the differentiation of the canal sense organs. They appear about the ampullary cristæ first, and only later grow toward each other to produce a common pocket. Consequently the conclusions of Krause and others who state that the posterior and anterior canals arise from *one* pocket are to be accepted only after such modifications as will bring them into harmony with the course of development known for them in bony fishes.

24. The semicircular canals may be said to be completely formed so soon as the lips of the folds have met and fused. The separation of the canal body from the utriculo-sacculus is a secondary process due to the resorption of the fused part of the lips of the groove. In most vertebrates this condition is soon assumed after the lips meet, and persists throughout life; but in Petromyzon the tissue intervening between the utriculo-saccular walls and the canals is not so soon nor so completely resorbed, which accounts for the closeness with which the canals are applied to the body of the ear in this animal.

25. A more exact determination of the absolute position of the ear with respect to the structures of the side of the head is now possible, and we find that the auditory vesicle is always developed

between the facial and glossopharyngeal nerves. (For Elasmobranchs, *cf.* Beard, VIII, Rep. Scot. Fishery Bd., 1889, Pl. X, Fig. 15; and for man, His, *Arch f. Anat.*, 1887, p. 376, Fig. 8.)

26. The *ear* progresses in its *ontogeny* according to the plan of development of the lateral line sense organs of the Ichthyopsida. There as here the appearance or disappearance of parts of the ear chamber are preceded, introduced, and governed by the division or death of the contained sense organs. The facts of development strengthen the conclusions drawn from comparative anatomy and show that the Cyclostome ear is the forerunner and an ancestral stage of the Gnathostome ear, and Retzius's idea that an impassable chasm exists between the ears of the two types is proven to be incorrect.

27. It is in the highest degree probable that the sense organ which I have discovered in the endolymphatic duct or surface ear canal of Petromyzon's ear exists also in the reptilian ear at least during ontogeny, *for its nerve is well developed in the saurians and passes into the wall of the endolymphatic duct.*

28. Hensen, among others, advocated the idea that the large epithelial ridge of the embryonic cochlea was the organ whose function it was to secrete the membrana tectoria, and most authors since his time have accepted this idea without question, notably Retzius. It has been taken for granted that all of the membrana tectoria of the embryo was converted into that of the adult, but that such a process does not occur is of course perfectly evident when one follows the resorption of the Sauropsid organ; for as the latter disappears, its capillary structures disappear with it, and the adult mammalian hair band is made up of the hairs springing from the smaller epithelial ridge alone. The embryonic membrane of Corti is made up of hairs of both large and small epithelial ridges, while the adult membrane is the product of the small epithelial ridge alone or in terms of adult anatomy; the embryonic "membrane" includes the product of both the transient Sauropsid organ and the permanent organ of Corti, while the adult "membrane" is of course the persistent portion of the embryonic membrane borne by the cells of the small ridge which constitute the hair cells of the adult organ of Corti.

Recapitulation E.

29. The vertebrate ear is a relatively late acquisition, phylogenetically speaking, and among the Sauropsida and Mammalia it offers the only remnant of the canal organs of their ichthyopsid ancestors.

30. The outcome of the survey of the anatomical and embryological fields is the conclusion that the surface territory out of which the ear developed was the best offered by the anatomical conditions of the ancestors of present vertebrates, and that the superiority of the territory chosen by natural selection over any other portion of the surface of the body lay in its combining in small space two, and that differently innervated, sensory apparatuses of a kind suitable for the further perfection of the function of the perception of wave motion. Among the higher forms the semicircular canals are degenerating, and one canal organ, the crista abortiva, has entirely disappeared. Corti's organ is not the papilla basilaris, as Retzius concludes, in agreement with Hasse and other anatomists, but only a small portion of it which has undergone peculiar modifications.

31. The auditory organs of invertebrates are not the forerunners or the ancestral forms of the vertebrate auditory organs, but they are differentiated structures which are confined strictly to the invertebrate group. It is of course possible that other sense organs of the invertebrate body have developed in the course of descent into the canal organs from which the vertebrate ear arose, but on this topic I have nothing to add to the opinions already expressed by other investigators.

Recapitulation F.

32. The functions of the ampullar sense organs and their connected canals can hardly be different from the sense organs of the lateral line, except in refinement of function; *i.e.* the difference can only be one of degree and not of kind. The highly modified line of cochlear organs has certainly carried the refinement of function much further, but it is not indicated anywhere that a different *kind* of function has been added to or substituted for the ancestral function.

The careful comparative study of the internal ear in its rela-

tions to the brain shows us that the semicircular canals do not now and never have possessed any special relations to the equilibrative function. In any case we cannot lose sight of the *primitive function* of the organs which gave rise to the ear organs. For the functions have probably not suffered greater alterations than the structure of the organs, and the changes in the latter have not been excessive, much less fundamental.

33. From all the evidence it appears that a vertebrate may live in perfect equilibrium without an internal ear. This is proven beyond question by Amphioxus, which has no ear, and by many forms among the lower vertebrates which may be deprived of their ears without *destroying or even disturbing* the powers of equilibration; *e.g.* Boettcher's *Frog*, Tomascewicz's *Carp*, and Steiner's *Sharks*.

34. If there are still those who cling to the old idea of a localization of the equilibrative function in the semicircular canals of the ear, it should suffice for their conversion to remind them that in low vertebrates, canal organs are placed on the surface of the body in all three planes of space and in planes oblique to these, and that these canals and their inclosed sense organs are subject to much greater motion in the planes of space, owing to their greater distance from the axis about which the motions which affect them and the ear canals alike are executed, and further, the surface organs are more subject to external sensory impressions than the inclosed ear canals (not considering the probably greatly heightened sensitiveness of the latter), so that these forms would not need the ear canals as equilibrative organs; but they are the *very ones which have the ear canals the best developed!*

35. As regards the canals themselves, they are not known to have any other function than the one inherited from their ancestors, viz. that of serving as mechanical protectors of the sense organs. The ear canals belong in the list of organs which continue to appear in ontogeny after the need which they were originated to fill has passed away. They are to be classed with such structures as valves in the horizontal veins of man's body, the vermiform appendix, coccygeal bones, atavistic muscles, and the rest of the considerable number of "normally" present but antiquated and functionless organs.

36. As a good example of how simple tactile corpuscles may

be made to serve in place of the higher sense organs for the orientation of the body, we may take the nasal sensory apparatus of the common mole (Eimer, 79, 1871), or, better still, that of the star-nosed mole (*Condylura cristata*). I have described in another place (6, 1885), the unusual nasal rays of this animal. This remarkable tactile apparatus is undoubtedly produced in response to needs of the animal, owing to its practical loss of sight, and it serves admirably to orient the body in the subterranean passages in which this mole lives.

Many more such facts might be brought forward to strengthen the view that the equilibration of the body is the product of the total of the activities of the nervous system acting over the whole periphery of the body, and is not the result of the activity of any special organ or group of organs such as the semicircular canals.

37. The filaments of the hair band meet the physical requirements of acoustics for the perception and transmission of the "waves" of auditory stimuli.

38. Timbre or the tonal color of sounds is due to a combination of the stimuli or the effects of the excitation of a series of vibrations of which the main or fundamental tone is most prominent, while the other vibrational impulses make themselves felt as "coloring" of this base. The combination is a psychical phenomenon, and there is no combined result of simultaneous, sympathetic vibrations transmitted from the ear; on the contrary, each vibrational impulse is transmitted to the brain at its full value, and its effect in audition is due entirely to psychical processes.

39. In the dog, according to Foster, the average pressure in the cerebro-spinal fluid is equal to 10 mm. of mercury, *i.e.* about one-tenth to one-seventeenth of the carotid pressure; and since the cerebro-spinal spaces communicate with the auditory channels (even though indirectly), this degree of pressure must be very near that under which the structures of the internal ear are called upon to carry out their functions, — a physical condition which should be kept in mind while dealing with the physiology of the ear sense organs in the Mammalia.

40. The function of the cochlea is carried out by the hair cells of the cochlea, which bear the long, slender, percipient hairs in such fashion that the waves of the endolymph are readily

propagated down the filaments to the sentient protoplasm of the sensory cells, which are directly continuous with the nerve fibres of the cochlear nerve. These are the only structures of the cochlea directly concerned in the picking up and transmitting auditory stimuli to the brain. Waves of the endolymph are propagated continuously through the canal, and the auditory hairs are consecutively affected thereby, as a result of which the psychical phenomena of audition depend upon a series of stimuli from the sensorium varying in intensity and frequency and number with the sound waves which gain admittance to the endolymphatic fluid.

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I. EXPLANATION OF THE FIGURES.

LIST OF REFERENCE LETTERS.

a.,	ampulla.
ac.,	acoustic nerve.
a.v.,	auditory vesicle.
b.,	pars basilaris cochleæ.
c.,	canal.
c.a.,	canal, anterior.
c.h.,	canal, horizontal.
c.p.,	canal, posterior.
d.,	ductus endolymphaticus.
e.,	eye.
f.,	forebrain.
g.,	branchial region.
h. and *h'*,	hind brain.
l.,	lagena and pars lagenæ cochleæ.
m.,	midbrain.
m.a.,	crista acustica.
m.s.,	macula sacculi.
m.u.,	macula utriculi.
n.,	nerve.
n.',	cristica acustica ampullæ.
n.'',	macula neglecta, or crista acustica abortiva.
p.,	ampulla of posterior canal.
p.o.,	canal pore.
s., *sc.*,	sacculus.
u., *U.*,	utriculus.
v.,	vesicle.

EXPLANATION OF PLATE I.

FIG. 1. The left internal ear of *Dasyatis centrurus*, seen from the outside, slightly enlarged. *x.*, the utricular canal or appendix from which the anterior and external canals are given off. Opposite the letter the channel of communication. *z.*, the saccular appendix and connecting canal. The connecting canals are not symmetrically placed with reference to the endolymphatic duct. *ab.*, nerve of the abortive canal organ which lies in *z*. *r.l.*, lagena nerve; *r.s.*, saccular nerve, etc. The lagena and post. ampulla appear in the figure in contact. They are separated by a considerable space, which here disappears in perspective. Osmic acid preparation.

FIG. 2. The right internal ear of *Carcharias littoralis*, seen from below and outside, to show the distribution of the nerves. Natural size. The cartilaginous case is partly dissected away, but sufficient remains to illustrate the relation of the membranous ear to the supporting structure. The relative sizes of the ear canals and the channels in the cartilage are clearly shown. Osmic acid preparation.

FIG. 3. The left ear of *Torpedo occidentalis*, seen from below and outside, showing the nerve distribution. The dorsal portions of the ear are not represented, and only part of the nerve end organs. Natural size. The splitting of the saccular nerve into two parts, one of which supplies the lagenar organ, is shown. Osmic acid preparation.

FIG. 4. A view from below of the nerve supply of the ear of *Petromyzon marinus* in its main branches. *g* VIII + *ac*, the auditory ganglion with which the accessory nerve is closely connected; *r.p.* and *r.a.*, the posterior and anterior branches of the so-called auditory with their two main branches. *r.a.c.* VIII, the accessory branch of the facial supplying the facial sense organ and the epithelial walls of the ear. The VII nerve appears in the figure to lie upon the VIII and its ganglion, but in reality lies between the observer and the VIII, and only traverses the auditory capsule.

FIG. 5. A sketch of the apparent origin and cranial exit of the V, VII, VIII, IX, and X nerves of *Carcharias littoralis* from the right side, seen from within. The brain has been raised and displaced to the left, so that only the ventral border of it is visible. The peripheral approach of the acustico-facial and the glossopharyngeal trunks is apparent even within the cranial wall.

FIG. 6. A very young embryo of *Acanthias vulgaris*, seen from the right side, illustrating the early appearance of the auditory saucer. The relation of the auditory sensory thickening to the remaining superficial sense organs is not here shown. × 20.

FIG. 7. Two figures of the internal ear of a 2.5 cm. embryo, *Galeus canis*. × 30. The ear sacs are compressed laterally. The separation of the sense organs is in progress, and all their important canal chambers are indicated at this early stage.

FIG. 8. Internal ear of a 2.5 cm. *Galeus canis* embryo, to illustrate the formation of the canals. × 35. The stage of development shown in this figure precedes by a short time the condition shown in Fig. 7, and the endolymphatic duct is relatively larger.

FIG. 9. Sketch of the internal ear of the left side of a 63-day *Salmo fario* embryo, to illustrate the manner of the formation of the semicircular canals, after von Noorden. The elliptical folds are about to fuse, thus completing the primary arch over the sense organs of the ampullæ. The latter are well-formed hills of hair-bearing sensory epithelium before they are thus inclosed. *o.*, otoliths, of which there are two groups of small and one large one present.

FIG. 10. Sketch of the nerve branches of the ramus anterior of the auditory

nerve of an adult *Raja erinacea*. × 5. The branching of the utricular nerve indicative of division of the original sensory patch is well shown. Osmic acid preparation.

FIG. 11. The two rami of the auditory nerve of *Myxine glutinosa* and their branches, after Retzius. × 18. The rami anterior and posterior supply respectively the utricular and saccular chambers of the ear, neither one crossing the line of separation marked out by the endolymphatic duct.

FIG. 12. Horizontal section through the auditory capsule of *Lacerta* embryo, after Hoffmann. × 50. The position of the vesicle is seen to be between the VII–VIII and the IX nerves, which come into immediate contact with the walls of the vesicle at this stage of development.

FIG. 13. Horizontal section through the ear of *Petromyzon marinus*, to illustrate the relation of the ramus accessorius of the facial nerve to the ventral walls of the ear. In sections dorsad of the one figured, the nerve rises nearly vertically in the sulcus frontalis, and gives off a branch to the sense organ in the commissural chamber, but its main portion is continued outward to the *surface canal* organ, which it supplies. For a considerable part of its course the nerve runs parallel and more or less closely applied to the ramus anterior of the auditory proper. × 70. *c.*, the outer walls of the connective tissue sheath of the ear. *r.ac.* VIII, the accessory branch of the facial.

FIG. 14. A transverse section through the ear of a young *Petromyzon Planeri*, near the middle of its vertical diameter. The section passes through the two endolymphatic ducts, the canals and ampullæ where the latter open into the utricular and saccular compartments. × 25. *cr.ac.*, the sense organs of the anterior and posterior ampullæ. *c.c.*, the cartilaginous capsule.

FIG. 15. A surface view of the superficial sense organs of the lateral line system of the Dogfish (*Galeus canis*), illustrating their relation to the auditory sense organ canal or endolymphatic duct. The auditory organ is subject to a precocious development, but retains its relation to the surface of the body and to its superficial relatives for a long time after disappearing from the surface; and, as shown in the figure, retains its place in the line of sense organs, connecting the lateral systems over the aural region. × 20. *o.d.e.*, the obliquely placed mouth of the endolymphatic duct; *au.g.*, the groove of modified epidermal epithelium (ectoderm), which reaches to *a.s.o.*, the point at which the auditory organ first made its appearance on the surface of the body.

FIG. 16. A dissection of the surface and ear canals of an Elasmobranch (*Rajoid*) embryo, probably Torpedo. × 10. The ears are revolved somewhat inwards and backwards on their endolymphatic ducts, in order to show their canals to advantage, but otherwise the parts are in their relative positions as viewed from the dorsum. The ears communicate by means of their endolymphatic ducts with the large subdermal sac, and these by means of the tubes *d.e.*, ordinarily described as the continuation of the endolymphatic ducts, with the exterior opening on the surface of the head at the points *p.ac.*, or the pori acustici, from which points grooves are continued to † in the transverse line of sense organs, out of which the auditory organ migrated at the beginning of its involution. *s.e.*, endolymphatic sacs; *o.c.*, occipita canal or line of sense organs; *c.s.o.*, canal sense organ. The pink elevations *s.s.* in endolymphatic sacs indicate the position of probable sense organs.

FIG. 17. The crista abortiva of an adult *Raja ocellata* showing a supernumerary bipartite sense organ with distinct nerve branch. × 3. Osmic preparation.

FIG. 18. A surface view of the external openings of the endolymphatic duct of *Raja ocellata*. × 2.

EXPLANATION OF PLATE II.

FIG. 1. A horizontal section of the ear of *Petromyzon marinus*, through the middle of the vertical diameter of the saccular appendix or lagena, showing the bifurcate sense organ of the lagena, and the nerve supply. × 45. *c.*, the cupulæ terminales of the sense organs.

FIG. 2. A vertical section through the posterior ampullar sense organ of the Petromyzon ear, to show the mutual relations of sensory epithelium, canal wall, and nerve. × 140. *c.*, canal wall thickened where the nerve penetrates it to enter the sense cells, whose position is indicated by the pink shade, *cr.ac.*, *r.ac.*, and *r.ac.'* the accessory nerve in long and cross section.

FIG. 3. A transverse section (radial) of the cochlear organ and canal of the Rabbit, to show the usual relation of sensory hair band to the limbus sulcus spiralis in paraffine preparations. *, the region from which Fig. 5 is taken. †, the caps of three hair cells, pulled off and still in connection with the hairs. *c.p.*, Corti's pillars and the remnant of the organ of Corti. *m.r.*, membrana Reissneri. *s.i.*, sulcus internis. *c.n.*, cochlear nerve. *s.v.*, stria vascularis. *m.b.*, basilar membrane. *v.s.*, spiral or basilar blood-vessel. *h.b.*, hair band. × 150.

FIG. 4. Sketch of a section of the net of Loewenberg of the Rabbit in its relation to the sensory hair band. From the region of the lower outer angle of the hair band in such a section as is shown in Fig. 3. *r.w.*, the thickened rim or edge of the hair band known as Hensen's "Randwulst," here seen to be composed of fibres. *h.'*, the hairs of the outer hair cells. × 1400.

FIG. 5. A surface view of the net of Loewenberg from the region * of Fig. 3. × 850. The net appears to be composed of cords and threads of varying size, and the meshes are not only unequal, but also very irregular in size and shape. *h.*, unchanged hairs of the outer hair cells.

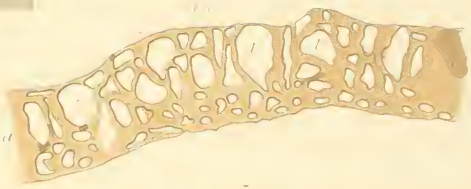
FIG. 6. Perspective view of the region † of the section of the hair band shown in Fig. 3, and more highly magnified. *ch.c.*, one of the caps of the outer hair cells which has remained in its normal attachment to the hair band, and which gives rise to 27 filaments or auditory hairs. × 850.

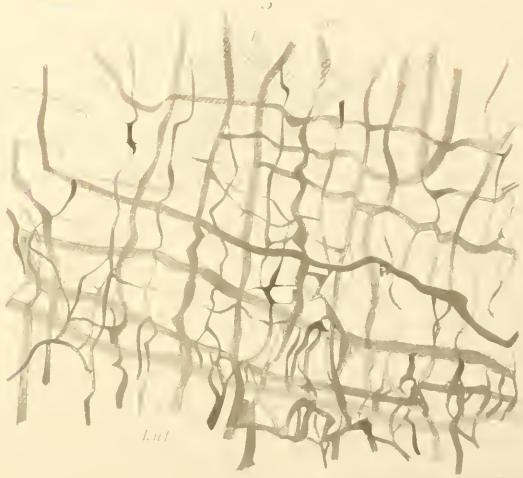
FIG. 7. (*a*) Surface view of the "Randkörpern" or "Randwulst" of the hair band, showing its reticulated structure, and (*b*) its relation to the sensory hairs in radial section. The preparation is taken from 10-inch Pig embryo. This appearance is not unusual, but the intermediate stages between this and the condition in which all traces of such structures are absent, as in the living and freshly prepared organs, are also abundant.

FIG. 8. The macula utriculi and the crista acustica of the anterior ampulla of the Opossum. × 30.

FIG. 9. Two supporting cells of the Sauropsid organ of the Alligator. × 440.

FIG. 10. Tangential (vertical) section of the endolymphatic sac of *Dasyatis centrurus*. × 15.





EXPLANATION OF PLATE III.

FIG. 1. A view in perspective of the developing organ of Corti of a Pig embryo 8½ inches in length. × 825. *l.e.r.*, the large epithelial ridge and its hair cells. The full complement of hairs to the cell is only indicated by the one hair, and only a small number of the hairs are drawn, for the sake of clearness. The figure illustrates the appearance of the organ during life. *s.n.*, the Sauropsid organ. *s.e.r.*, small epithelial ridge. The nerves and other parts are not indicated. For other detail of section, see Fig. 1, Pl. VI, and Fig. 2, this plate.

FIG. 2. A radial section of the cochlear canal and adjacent parts showing the relation of the developing organ of Corti to the canal and to its nerve. *s.e.r.* and *l.e.r.*, small and large epithelial ridges respectively. The latter is the Sauropsid organ which disappears by the time adult life is reached. Both organs are composed of hair-bearing cells, which at this stage are very much alike, although the future organ of Corti has begun its differentiation out of the small epithelial fold.

FIG. 3. A fragment of a group of auditory hairs of the sensory hair band of the organ of Corti of the Ox, isolated from the band, and partly teased out. × 850. The figure illustrates the size and regularity of the capillary filaments, and the absence of an intermediate imbedding substance.

FIG. 4. A view of the ventral surface of the hair band of the Ox, to illustrate the manner in which the plate breaks away from the hair cells. The crenulate line crossing the band from right to left is the inner half of the circular areas occupied by the hairs after being torn off the cells. Osmic-glycerine preparation. × 440. At *c.h.c.* the cap of one of the hair cells remains, and the hair ends may readily be counted.

FIG. 5. Surface view of Loewenberg's net in its relation to the dorsal surface of the sensory hair band of the Rabbit. × 180. The figure illustrates one extreme of the complicated structures arising out of the destruction of the normal relation of the surface layers of the hair band. *i.h.b.*, inner border of the hair band, usually described as composed of amorphous substance.

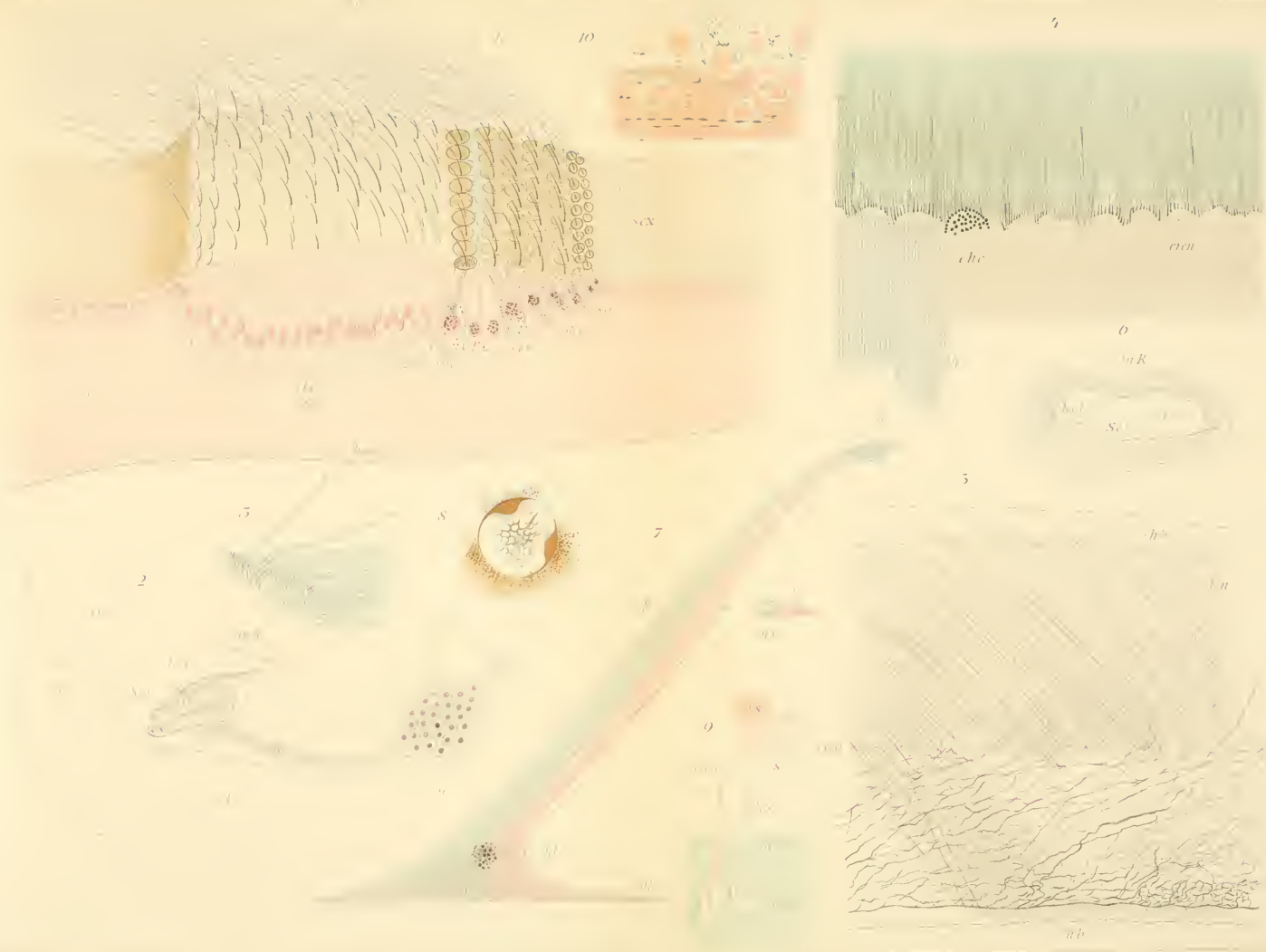
FIG. 6. Transverse section of the cochlear canal of a 2¼-inch Pig embryo, to show the epithelial ridge (*l.e.r.*), out of which the organ of Corti is developed, and the other ridges, which for the most part disappear during later development in the mammal. × about 350.

FIG. 7. Side view of one rod of Corti of the Rabbit, showing the continuation of the cell protoplasm up to the pillar head, and its penetration in between the spreading fibres of the foot plate. The small figure at the side represents a cross-section along the line "*c*," and shows that the bundle of fibres constituting the rod is inclosed in the common sheath of the protoplasm. × 865.

FIG. 8. A surface view of the outer end of an endolymphatic duct in *Dasyatis centrurus*.

FIG. 9. The two endolymphatic ducts of *Sphyrna zygæna*. *d.e.u.*, utricular duct. *s.u.*, the sac of the utricular duct. *d.e.s.*, saccular duct. *s.s.*, its sac. *c.a.* and *c.p.*, anterior and posterior ear canals. *k.*, cartilaginous auditory capsule.

FIG. 10. A small portion of one of the so-called spiral nerve bundles. The first or innermost one of the outer hair cell territory. × 880. Methyl blue.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EXPLANATION OF PLATE IV.

FIG. 1. Surface view of the apical turn of the cochlear spiral of the common Mouse, to illustrate the twisted condition of the cochlear organ. × 30. *a.c.c.*, apex of cochlear organ, its distal end. *c.n.*, the cochlear nerve. *c.c.*, cochlear canal. *b.m.*, basilar membrane. *h.b.*, hair band. *l.s.o.*, lamina spiralis ossea. *st.v.*, stria vascularis. At *c.n.* and *n.* the variation in the amount of spiral twist which the terminal bundles of the cochlear nerve suffer is well shown. The canal is not curved equally in all its parts. The figure shows three different degrees of curvature.

FIG. 2. Transverse section of the cochlear canal and contained structures of a new-born Rabbit. × 85. *Lg.s.*, ligamentum spirale. *Sc.t.*, scala tympani. *sc.v.*, scala vestibuli. The epithelial ridges are colored red; the hair band, brown. In the canal is seen the remains of hair structures from source unknown.

FIG. 3. Transverse section of the organ of Corti of new-born Rabbit, to show the relations of the cellular constituents of this stage of development. × 865. There are shown five rows of well-developed hair cells, and four rows of supporting cells, which at this stage are also hair-bearing. The hair cells of the Sauropsid organ are very numerous. *c.p.c.*, embryonic Corti's pillar cells.

FIG. 4. Four figures of transverse sections through the auditory region of the head and through the auditory capsule of early embryos of *Petromyzon fluviatilis*. After Kuppfer.

a. Through the ingrowing ear cup and facial ganglion. The double lip of the upper wall of the cup is well marked.

b. A later stage of the auditory involution, viewed in transsection through the middle of its longitudinal diameter. The opening through the ectoderm is still persistent — endolymphatic duct. The "dorsal root" is seen to enter the gap in the top of the capsule.

c. Transverse section, to show the manner of nerve ending of the "dorsal root."

d. The same, more highly magnified.

FIG. 5. Three figures of transverse sections of *Lacerta viridis* embryos, through the internal ear in three stages of its development. After Hoffmann. The membranous ear is colored red; the nerve, black.

a. × 36. Through an early stage of canal formation and ampulla building. The cochlear nerve and ganglion are in contact with the outgrowing cochlear tube.

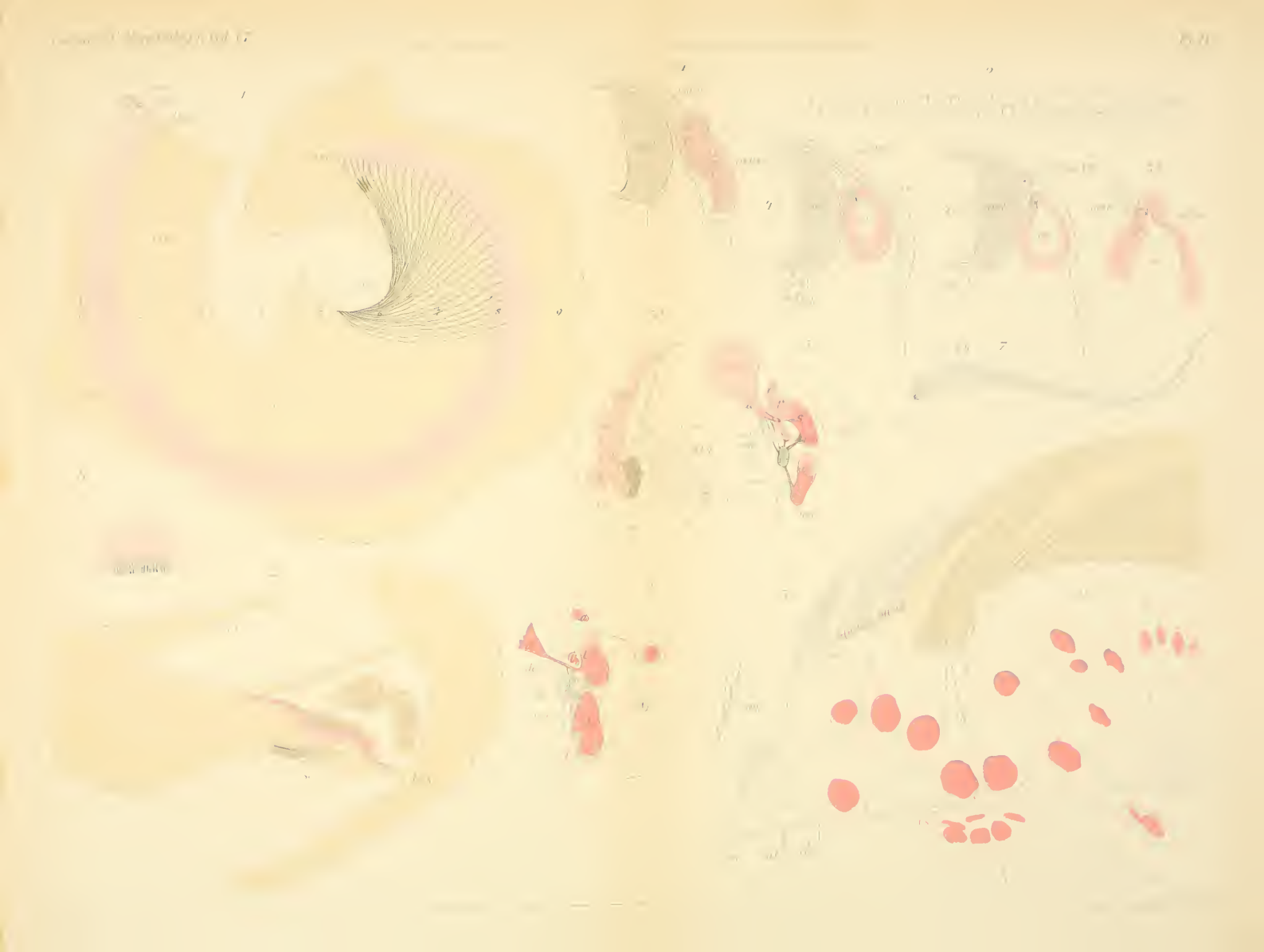
b. A late stage of the developing ear, to show the manner of branching of the nerve and its distribution to the parts of the ear. *r.d.e.*, ramulus supplying the ductus endolymphaticus.

c. A still later stage of the same.

FIG. 6. Camera sketch of the apex of the arch of Corti of the Dog, to show the relative sizes of the outer (upper in figure) and lower pillar heads. × 630.

FIG. 7. The hair band of a young Virginia Opossum in transsection, to show the shape, breadth, and thickness, and also one condition of the appendix (Randwulst or Körper) to the outer edge. × 630.

FIG. 8. Horizontal section of the cochlear organ of *Petromyzon marinus*, below its bifurcation. × 45.



EXPLANATION OF PLATE V.

FIG. 1. A surface view (dorsal) of the organ of Corti of the Virginia Opossum. *a*. × 630, *b*. × 380. *a*., the heads of the outer pillars of Corti prolonged into the apical beaks *o.p.h.* and the outer face of the arch *c.a.* *s*., spaces between the heads occupied by the first row of outer hair cells. *b*., surface view of the hair band. The length and course of the hairs in four successive planes shown. *h.c*., hair cells. *l*., lumen in the inner edge of the band, — the so-called structureless edge. *l.k*., outer edge of band.

FIG. 2. The caps of three hair cells from the organ of Corti of an adult Rabbit. The basal ends of the auditory hairs remain attached to the cap, and are shown in the figure only on one of the cell caps. Some of the hairs are much bent and curled, owing to elastic rebound after the breaking strain had been applied. × 1400. NaCl, glycerine preparation.

FIG. 3. A view from the dorsal surface of the organ of Corti of a Rabbit newly born, showing the long hairs of the organ of Corti in connection with their cells. The cells of the first two rows of outer hair cells are the only ones shown in the figure. × 850. The brown background represents the body of the hair band, and at *h.b.* the course of the upper layer of fibres or hairs is shown. *h.c*., hair cells. In the figure "Cortis fillars" should of course read "Corti's pillars," the double outline indicating the position of the row of pillar heads.

FIG. 4. A portion of a tangential section of the organ of Corti of an adult Rabbit, showing the manner in which the hairs of the hair cells pass off to the hair band. The structure of the hair cells is shown in two of them. × 1400. *s.c*., supporting cells. *nl.cl.f*., the nucleo-capillary fibres connecting the roots of the hairs with the nucleus.

FIG. 5. Three hair cells from the adult organ of Corti of the Rabbit, showing the "Hensenschenkörper" and its relation to the auditory hairs on the one hand and the nucleus on the other. × 1400. In *a*, at *do* is shown the manner of entrance or attachment of the nucleo-capillary filaments to the nucleus. They cross a shrinkage space in the protoplasm just before attaching.

FIG. 6. A perspective view of the developing organ of Corti of a Pig embryo 10 inches in length. Showing the manner in which the auditory hairs rise from the surface of the epithelial cells. × 114. *l.e.r*. and *s.e.r*., large and small epithelial ridges.

FIG. 7. An auditory cell from the organ of Corti of an adult Rabbit, showing the relation of the hairs to the cell, and especially its nucleus, as in Fig. 5. × 1400. The hair filaments are continued from without through the cell. The "Hensen Körper" lies at the base of the apical funnel of the cell. The nerve enters the side of the cell. The figure does not intend to convey the idea that the nerve enters the nucleus.

FIG. 8. A nucleus of an auditory cell from the same organ of Corti, showing the capillary filaments of the peripheral and neural poles of the nucleus and two lateral stainable bodies. × 1400.

FIG. 9. Transverse section of the developing organ of Corti of a Pig embryo $8\frac{1}{2}$ inches in length. The pillar cell has not yet divided. × 380. The hairs of the

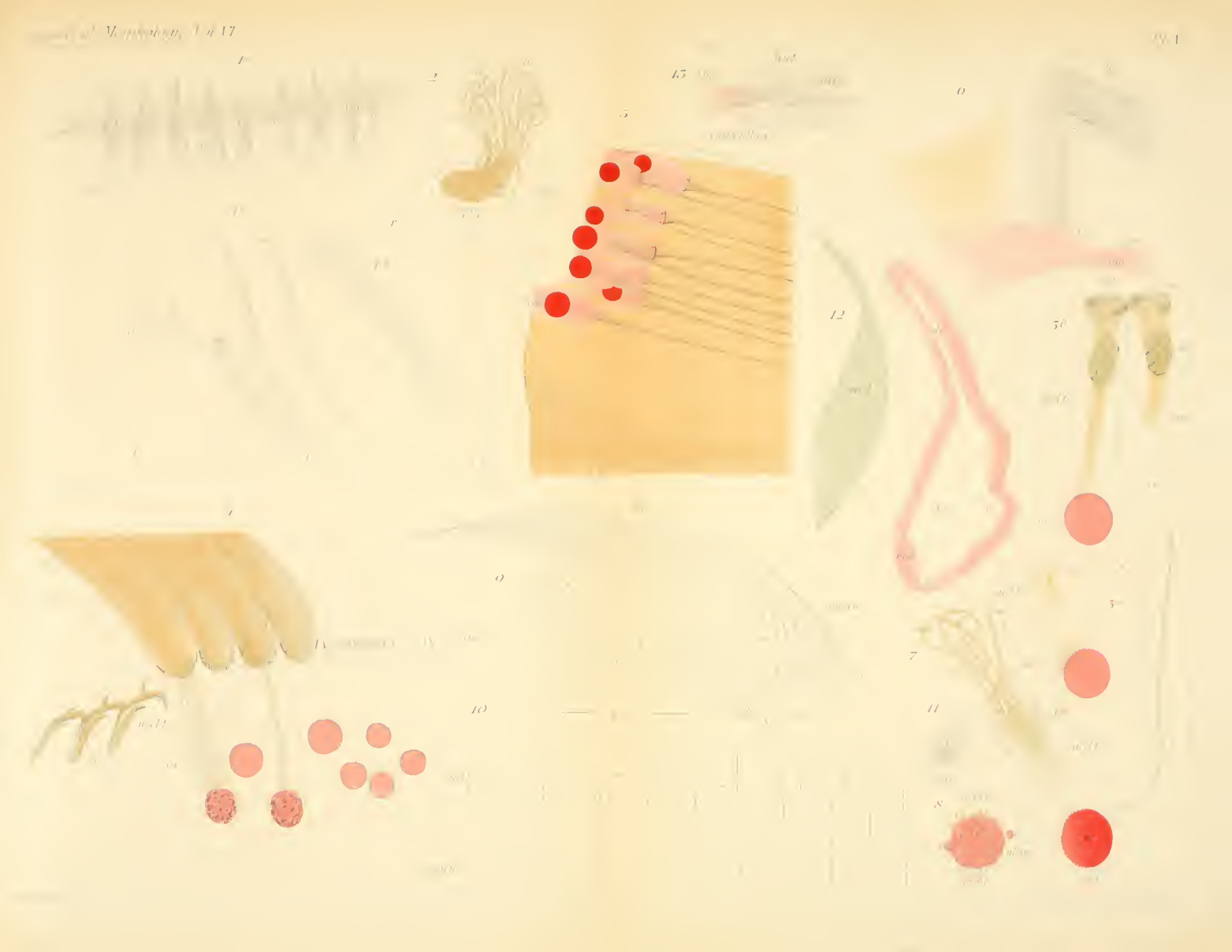
cells of the large epithelial ridge are shown to form part of the hair band, and are well developed at this stage.

FIG. 10. Surface view of the pillar heads of Corti's rods, showing the relative sizes and numbers. From the adult Rabbit. × 1400. *i.*, inner, *o.*, outer, pillar head.

FIG. 11. A hair cell with short hair; basal remnants adhering to its cap. Rabbit × 850. This figure is very much like those published by Gottstein and Waldeyer. Chromic acid preparation.

FIG. 12. Transverse section of ear sac of *Torpedo marmorata* embryo 1¾ cm. in length, showing the beginnings of canal development in the ear, and the relation of the endolymphatic duct to the sac. × 114. *m.u.*, the utricular sense organ. *e.c.*, external canal.

FIG. 13. One of the openings of the habenula perforata and the transmitted nerve of the Dog, seen slightly obliquely. × 1065. The nerve, before it enters the membrana basilaris, stains red (its sheath). The rest of its distal portion unstained, and composed of axis cylinders only.



EXPLANATION OF PLATE VI.

FIG. 1. A transverse section of the cochlear organ of an 8½-inch Pig embryo. × 285. *s.e.r.*, *l.e.r.*, small and large epithelial ridges. *c.c.*, cochlear canal. *s.c.*, supporting cells. *h.b.*, hair band. *c.n.*, cochlear nerve. *g.c.*, cochlear ganglion. *m.b.*, membrana vasilaris. *c.p.c.*, Corti's pillar cell, which has not divided into the inner and outer cells. *s.t.*, scala tympani.

FIG. 2. Transverse section (radial) of the cochlea of the house Mouse (adult). × 114. To show the length and relation of the hairs of the hair band. *o.c.*, organ of Corti. *s.v.*, scala vestibuli. *s.t.*, scala tympani. *s.v.*, stria vascularis. *m.R.*, membrana Reissneri.

FIG. 3. The apical spire of the cochlea of a 19 cm. Pig embryo. *o.c.*, organ of Corti. *c.c.*, Corti's canal; the arrow lies over the lamina spiralis ossea, magnified about 20 diameters. *l.*, the apex of the epithelial ridge. No helicotrema is developed.

FIG. 4. The distal end of the cochlear tube of the Mocking-bird, with the lagenar bulb. *l.c.*, *c.*, and *c.'*, the cartilaginous framework on which is stretched the membrana basilaris (*m.b.*). *o.m.*, the otolithic mass lying over the lagenar sense organ. × 90.

FIG. 5. Surface view of three cochlear sense organs from the adult human ear. *i.c.*, inner hair cells. *oc.*^{1}–*oc.*^{4}, rows of outer hair cells. The rows of sense cells are seen to be more and more incomplete the further they are removed from the inner edge of the organ. Only the outlines of the hair-cell caps are drawn in. After Retzius.

FIG. 6. The lageno-cochlear tube of the Mocking-bird seen from its neural face. *n.p.b.*, n. papilla basilaris. *b.v.*, blood-vessel. *r.l.*, ramulus lagenæ n.p.b. cochlear nerve. *o.m.*, the otolithic mass lying over the lagenar sense organ. *c.c.*, cochlear canal. *b.*, the isolated otolithic mass, to show its zones and peculiar shield shape. *c.*, to illustrate the tortuous course of the main vascular trunks in the roof of the cochlear canal or the stria vascularis. × 10.

FIG. 7. Surface view of the sensory hair cells of the basilar organ of the Mocking-bird's ear. × 1400. *h.c.*, hair cell. *h.*, one of the several hairs springing independently from the top of the cell. *s.c.*, supporting cell.

FIG. 8. Surface view of ampullar sense organ of the Mocking-bird. × 45. Showing the several crests composing the crista acustica. *p.c.*, projecting axial crests. *a.c.*, apical crest. *p.s.*, planium semilunatum. *c.w.*, canal wall.

FIG. 9. A view of the auditory hairs from five hair cells of the papilla lagenæ of the Mocking-bird. × 850. *a*, the hairs, more or less torn and spread into a brush. *b*, *c*, and *d*, normal slender hairs. *e*, an exceptionally strong hair. Living preparation.

FIG. 10. An oblique view of a piece of the membrana tectoria or hair band of the Mocking-bird. *e.p.*, epithelium. *a*, the general course of the striations and lines of lacunæ. *l.*, the perforating lacunale of the band. × 510. Chrom-osmic preparation.

FIGS. 11 and 12. The acustico-facial nerves and ganglia of a human embryo 22 mm. long. × 25. The figures are drawn from a model of these structures as found on the left side. After W. His, Jr.

FIG. 11. Seen from in front.

FIG. 12. Seen from behind.

a–b., a piece of the brain cortex — at *b*, the medulla wall. The portion central roots are figured, extending above this cortical strip.

c., lateral or cochlear root.

v., medial or vestibular root.

f., terminal portion of the facial root.

1, trunk of the vestibular nerve.

2, vestibular ganglion.

3, the vestibular nerve branch common to the two ampullæ. It bifurcates

4, into ramulus ampullæ anterioris,

5, and ramulus ampullæ externæ.

6, the branch to the maculæ recessus utriculi, showing its broadening out on the surface of the septum of the vestibule.

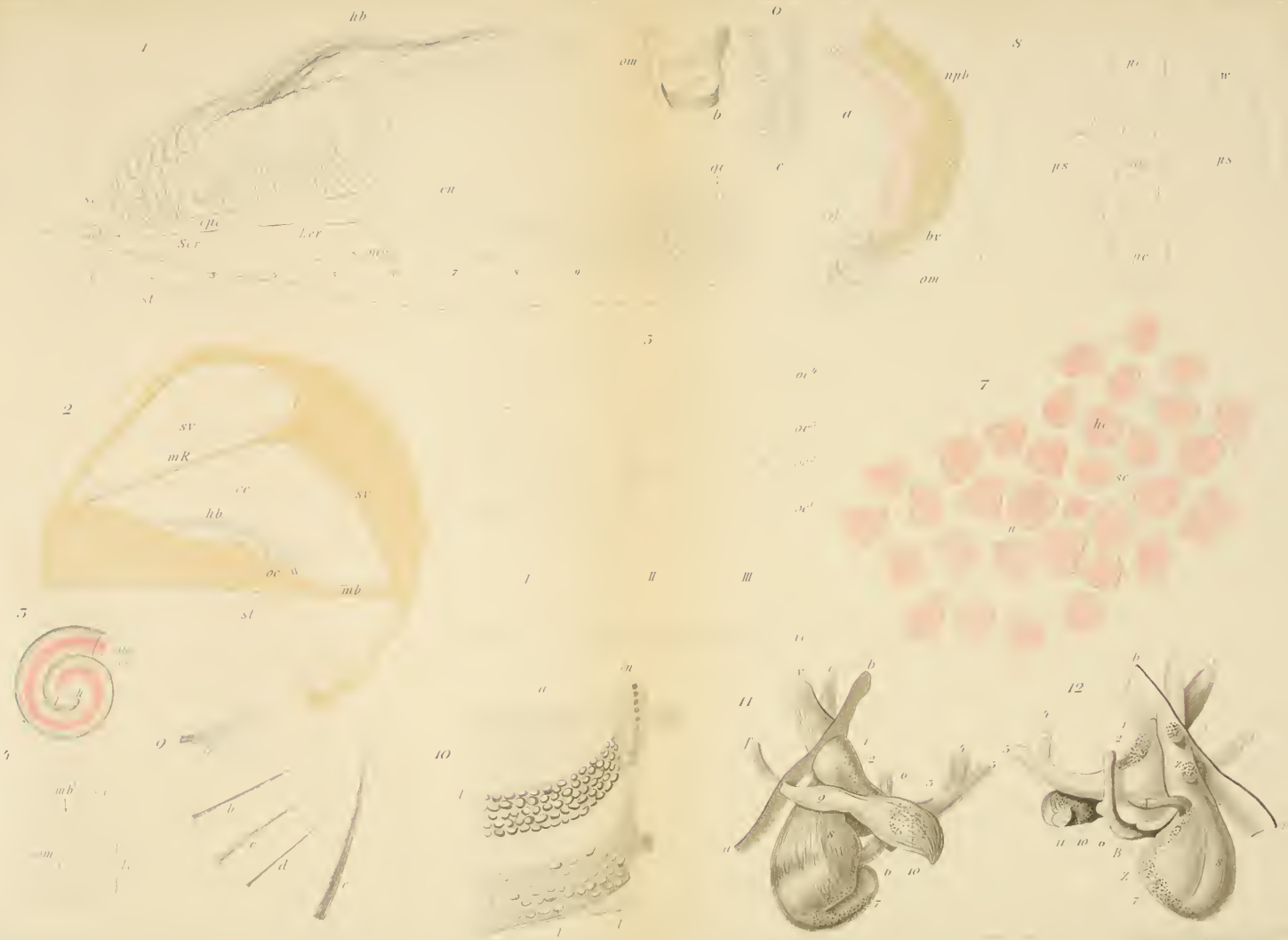
7, the cochlear ganglion.

8, trunk of the cochlear nerve; with *i.*, the intercranial ganglion, *z–z*, the intermediate ganglion. *A*, ramulus ampullæ posterioris. *B*, ramulus maculæ sacculi.

9, root of the facial nerve above the (10) ganglion geniculi.

10, ganglion geniculi.

11, trunk of the facial, cut through below the genu.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EXPLANATION OF PLATE VII.

FIG. 1. Several hair cells from the basilar organ of the Mocking-bird, to show the effect of reagents upon the hairs. *a*, the average result of the action of alcohol and hardening acids upon the hairs when care is exercised to preserve them. *b*, a nearly normal hair, with tip slightly melted down by the acid. *c*, more modified hair. *d*, an apparent collar about the base of the hairs of one cell. × 1400.

FIG. 2. One of the cartilaginous bars and the attached membrana basilaris from the cochlea of the Mocking-bird, showing the two very distinct fibre layers of the membrane. *v.s.*, spiral blood-vessel. *e.p.*, a few of the epithelial cells of the sense organ covering the membrane. 1 and 2, the lower and upper layers of the basilar membrane. × 380.

FIG. 3. Three hairs from the papilla lagenæ of the Mocking-bird, with their basal attachment, viewed in living condition in normal salt solution, with optical sections at *a* and *b*. × 850.

FIG. 4. The proximal end of the membrana basilaris and its frame, from the adult Mocking-bird. × 45. *h.c.*, hair cells of the basilar papilla. The shaded polygons have the hairs indicated. 1, 2, 3, the three layers of the basilar membrane. 2, the intermediate layer not shown in Fig. 2.

FIG. 5. Four hair cells from the papilla lagenæ. *a* and *b*, after the use of hardening reagents. *c* and *d*, in the normal condition. × 1400. From the adult Mocking-bird.

FIG. 6. A single hair cell isolated from the lagenar organ after the usual hardening method. The hairs broken off and separated. × 1400.

FIG. 7. The whole of the cochlear tube of the Mocking-bird, viewed from its neural face. *n.c.*, cochlear nerve. *r.p.b.*, ramus papillæ basilaris. *r.l.*, ramulus lagenæ. *c.* and *c.'*, cartilaginous frame. *b.v.*, blood-vessel. *s.c.*, superior transverse cartilage. The left ear from the inside.

FIG. 8. A single hair cell, alive in aqueous humor. *a*, terminal bulb of hair affixed to cover glass. *b*, the elastic hair. *c*, the cell cap.

FIG. 9. The same cochlear tube seen from the outside, on its vascular face. Letters the same as in Fig. 7.

FIG. 10. A nearly vertical section of the developing ear of a 32-day *Salmo fario* embryo. × 114. *d.e.*, ductus endolymphaticus. *m.d.*, the floor of the medulla. *m.o.*, the roof of the mouth. *c.r.p.*, *c.r.a.*, and *c.r.e.*, the three cristæ acusticæ, posterior, anterior, and external, respectively. *e.*, eye. The blood-vessels and lymph spaces below the cristæ are distinctly seen, as well as the nerve to the anterior ampullar sense organ, which appears in section.

FIG. 11. The crista acustica of the ampulla of the Mocking-bird, seen from the side. *a.c.*, *p.c.*, and *l.c.*, the apical, axial, and lateral crests of the structure, the latter passing out into the planum semilunatum. × 45. The sensory hairs cover the whole surface of the structure, but appear in this figure only around the edges.

FIG. 12. Three cells from the papilla basilaris of the Mocking-bird, to show the relation of the sensory hair to the surface of the cell during the action of reagents. × 2800. In cell *a* two hairs have not yet been affected, while all others have been melted down at their tips, leaving a bead of varying shape as the representative of the slender hair.

FIG. 13. Otolithic crystals from the papilla lagenæ of the Mocking-bird. *a*, *b*, *c*, *d*, the several shapes and sizes of the crystals observed. × 850.

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d

EXPLANATION OF PLATE VIII.

FIG. 1. A transverse section of the head of *Torpedo marmorata* through the auditory region, showing the relation of the endolymphatic duct to the auditory involution and the surface of the body. × 85. *ch.*, chorda dorsalis. *car.*, carotid artery. *md.*, medulla. *d.e.*, ductus endolymphaticus. *a.v.*, auditory vesicle. Embryo 1¾ cm. in length.

FIG. 2. A transverse section of the end of the endolymphatic duct taken from the same series as Fig. 1, but caudad of Fig. 1, showing the manner in which the ear canal opens on the surface of the body. *sp.*, tissue above the superior lip of the duct (primitive opening of the involution of the ear). *c.c.*, connective tissue cells. *ect.*, unmodified ectoderm. × 540.

FIG. 3. The same, from the next section. *o.de.*, mouth of the duct. × 380.

FIG. 4. The same, from the section next behind Fig. 3, showing the wide-open mouth of the ear duct. × 285.

FIG. 5. Surface view of the basilar membrane of the Virginia Opossum, to show its composition. *b*, *m*, *f*, *h*, the transverse fibres of the membrane. *b*, *m*, *f*, *l*, the longitudinal fibres above and below the former, which is in consequence the middle layer. The superficial layer of longitudinal fibres is the layer figured and described in part by Nuel, Deiters, and others as one of the bundles of longitudinal nerve fibres of the organ of Corti. × 1065.

b. Some of the longitudinal superficial fibres. × 850. From another part of the same ear.

FIG. 6. Surface view of the keystone of the arch of Corti and the pillar head prolongations. *h.o.p.*, *o.h.c.*, the hair cells of the outer series. *i.ch*, of the inner series. *s.*, spaces between the pillar heads. From the Opossum.

FIG. 7. A few isolated superficial longitudinal basilar membrane fibres, or so-called longitudinal nerve fibres of Deiters. × 1065.

FIG. 8. A small segment of the hair band from the ear of an adult Virginia Opossum. × 380. The figure shows the appearance of the atifacts, or so-called "Rand Körper" of Hensen, and the "Net of Loewenberg." *h.b.*, hair band. *L.n.*, net of Loewenberg. *C.p.*, Corti's pillars. *r.k.*, "Rand Körper."

FIG. 9. A single hair cell of the outer series from the ear of an adult Virginia Opossum. To show the relation of the hairs to the cap of the cell. × about 1400.

FIG. 10. Surface view of four of the inner and four outer pillar heads from the Opossum's ear. × 1400.

a.c., arch of Corti. *i.p.* and *o.p.*, inner and outer pillar heads.

FIG. 11. A transverse section of the sense organ in the larger surface canal of Petromyzon marinus. × 165.

FIG. 12. The nerve end in an epithelial (hair) cell from the same. × about 1000.

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hop
ihc
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EXPLANATION OF PLATE IX.

FIG. 1. A diagrammatic figure illustrating the sequence of sense organs or groups of sensory cells in the organ of Corti of the mammalian ear. The measurements are taken from the human ear, and the whole figure is magnified 8 diameters. 1 to 100 + the number of the cell groups, or sense organs. The distribution of the cochlear nerve and its breaking up into branches for the organs is taken from camera drawings. Anastomoses are not shown. *c.r.*, sacculo-cochlear canal. *c.c.*, cochlear canal. *c.n.*, trunk of the cochlear nerve.

FIG. 2. The Cyclostome type ear shown here is a very simple structure as compared with the complicated organ found among the *Gnathostomata*, but compared with its ancestral condition, *i.e.* the auditory vesicle, it is seen to have gone through many changes, and stands to-day midway between its earliest condition and the highest differentiation known. This diagram is constructed on the basis of the anatomy of the only two known forms of this group, *Myxine* and *Petromyzon*. The canals and their organ retain a very primitive condition of structure.

caa., anterior canal.
cap., posterior canal.
cr.a., crista acustica anterior.
cr.p., crista acustica posterior.
d., endolymphatic duct.
u.s., the utriculo-sacculus.
u. 1 and 2, branchlets of the utricular branch of the auditory nerve.
s. 1 and 2, the saccular branches of the same.
c.s., sense organ of the canal commissure.
n.ac.f., accessory auditory nerve.
ode., terminal portion of the endolymphatic ducts, which in neither of these Cyclostomes open on the surface of the body in adult life. Only one, the utricular duct, is represented as bearing canal organs, though it is nearly certain that both ducts are sense organ canals in Petromyzon.
mac.u., macula acustica utriculi.
mac.s., macula acustica sacculi.
1 and 2, the portions (1) of the sense organs that remain in the parent cavity and the portion (2) which migrate into the recessus utriculi and lagena respectively.

FIG. 3. The Gnathostome type ear shown here illustrates the method and the extent of the modifications which the Cyclostome ear has suffered in its descent to this group. The anterior and posterior canal organs have each budded off an organ which, in the case of the anterior canal, produces a well-formed canal, the external, present in all the members of this group, while the posterior bud never produces a well-formed canal. The utricular recess, which contains a number of sense organs derived from the division of the macula utriculi, is represented as forming a tubular prolongation of the utricular cavity, in order to more clearly show the parallelism of this group of organs with the lagenar group. In no known form does the production of the canal proceed to the extent shown in the diagram. The sense organs of the

lagenar group are represented as separated from each other by an interval, whereas the actual relation in nature is much more intimate.

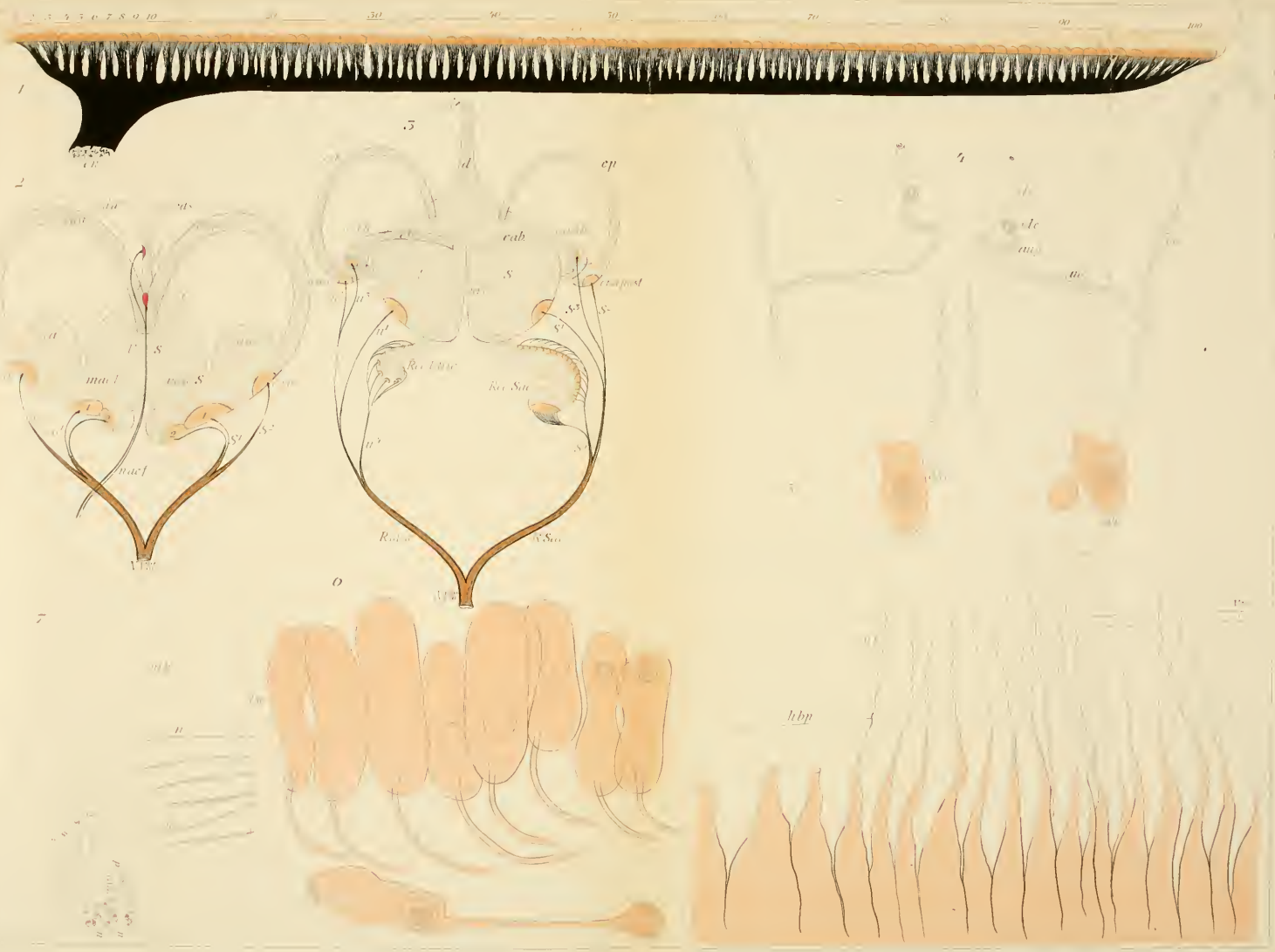
ca., anterior canal.
cp., posterior canal.
ch., external canal.
c.ab., abortive canal.
u. utriculus.
rec.utric., recessus utriculi.
rec.sac., recessus sacculi.
d., ductus endolymphaticus.
s., sacculus.
o.de., orifice of the same.

FIG. 4. A surface view of the relations of the invaginated ear to the superficial canal sense organs, in the ontogeny of the Spiny Dogfish, *Acanthias vulgaris*. × 20. *d.e.*, ear duct. *o.de.*, mouth of same, opening through the skin into the ear groove, *aug.* *au.c.*, the line of canal sense organs, crossing the head and connecting the two lateral systems, *o.c.*

FIG. 5. Surface view of the nerve plate which enters the membrana basilaris. From a preparation of the organ of Corti of the Dog, stained with alcohol carmine. × 1065. The nerve fibres are shown crossing the space arched over by the pillars of Corti, and reaching as far as the hair cells of the outer row. *n.f.*, non-medullated nerve fibres. *hb.p.*, line of the openings of the habenula perforata. *v.s.*, spiral vessel.

FIG. 6. A series of the hair cells of the organ of Corti of the Virginia Opossum. × 1065. The hairs are in large part removed, only one cell showing the basal remnant of these structures.

FIG. 7. The lower end of the basilar membrane and its bony framework, from the adult human subject. × 380. *n.*, the nerve fibres penetrating to the middle of the basilar membrane. *l.s.o.*, lamina spiralis ossea.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cp
cab
S
mac f
nacf
hbp

EXPLANATION OF PLATE X.

FIG. 1. A preparation of the organ of Corti of the Virginia Opossum in osmic acid, to demonstrate the course of the nerves across the arch of Corti. *g.*, ganglionic (?) varicosity of the nerve fibres, *n.* *c.p.f.*, foot of Corti's pillar. *nl.cp.*, nucleus of the pillar cell of the outer pillars. *p.*, projection from the apex of the arch. × 865.

FIG. 2. A view of the internal ear of *Petromyzon marinus*, from above and without, to show the relation of the sense organ to the commissural chamber and the manner in which the two endolymphatic tubes pierce the walls of the utriculus and sacculus respectively. *v.*, *v.'*, the utricular and saccular chambers. *c.a.* and *c.p.*, the anterior and posterior semicircular canals. *s.o.*, sense organ of the commissure. *c.*, commissural chamber, in which it lies. *d.e.s.*, ductus endolymphaticus utriculi. *d.e.u.*, ductus endolymphaticus sacculi. Owing to an inadvertence the *d.e.s.* of the figure was placed on the sacculus. It should occupy a corresponding place on the utriculus. *m.r.*, median raphe, but partly separating the two chambers of the ear. VIII *ac.*, the auditory accessory nerve which supplies the commissural and surface canal sense organs. × 20.

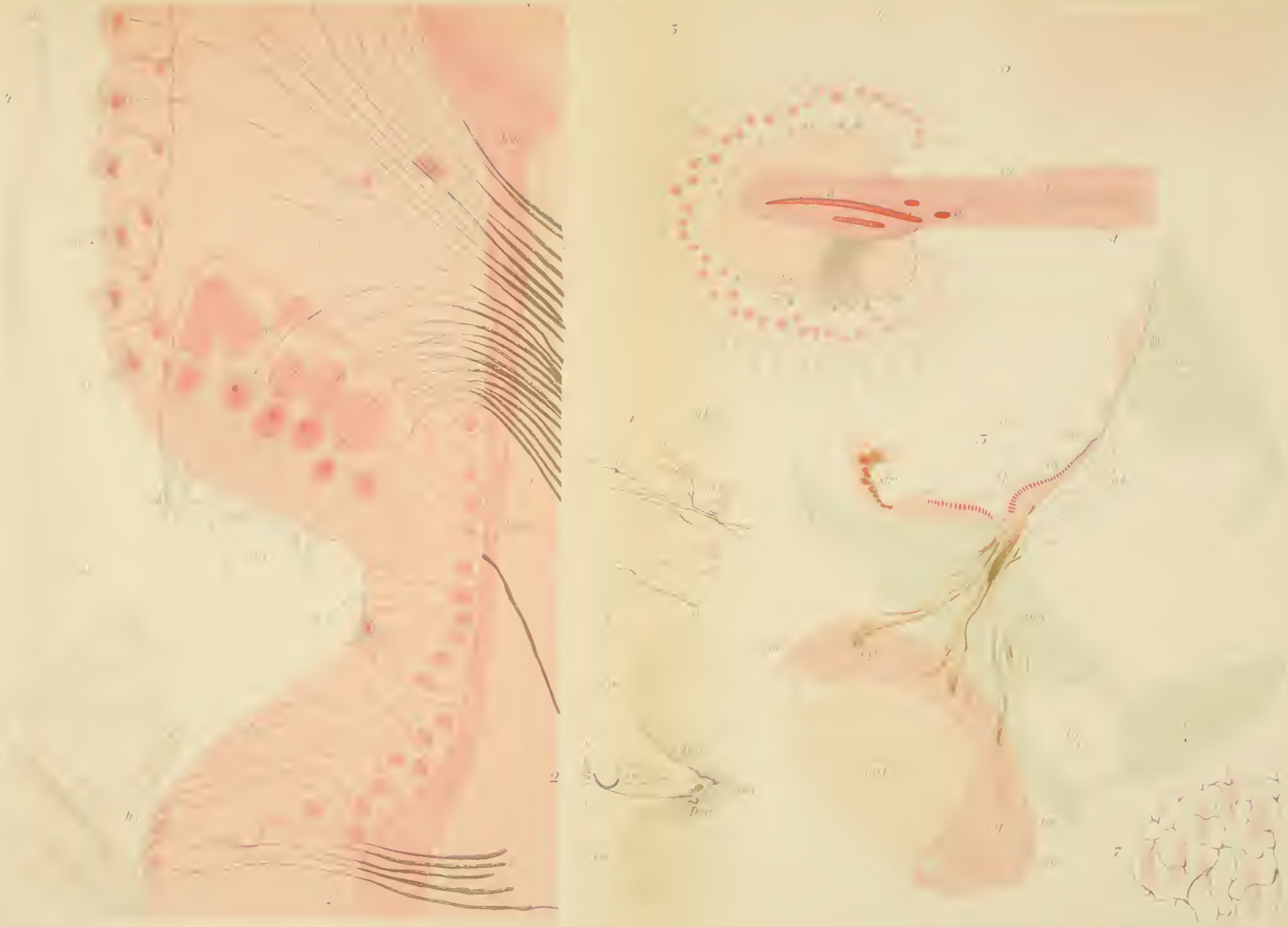
FIG. 3. Transverse section of the cochlear organ of the Alligator (*A. mississippiensis*), to show the relation of the parts. *c.n.f.*, cochlear nerve fibres. *c.n.g.*, cochlear nerve ganglion cells. *c.c.'*, cartilaginous bars framing the membrana basilaris. *l.e.r.* and *s.e.r.*, large and small epithelial ridges of the Alligator ear *e.e.'*, two apparently non-hair-bearing epithelial ridges. *b.v.*, blood-vessels. *s.t.*, scala tympani. *s.v.*, scala vestibuli. *c.c.*, cochlear canal. *h.b.*, hair band. *str.v.*, stria vascularis. *a.h.*, auditory hairs. *r.p.b.*, ramulus papillæ basilaris n. cochleæ. *v.s.*, spiral vessels. *c.a.*, cochlear artery. *sh.*, sheath of cochlear nerve. × 30.

FIG. 4. A small portion of the preceding figure more highly magnified, to show the hair band and its composition and relation to the short hairs still connected with the sensory cells. *a.h.*, auditory hairs. *h.c.*, hair cells. *sp.c.*, supporting cells. *h.b.*, hair band. *ah.'* and *ah.''*, the free ends of the auditory hairs projecting beyond the bounds of the hair band or membrana tectoria, which has been torn from its attachment to the hair cells. *n.*, nerve fibres. *b.m.*, basilar membrane.

FIG. 5. A horizontal section of the sense organ of the commissure from the Petromyzon ear. *s.t.*, supporting stalk of the sense organ. *h.c.*, hair cell. *e.p.*, non-sensory epithelium. *b.t.*, basement tissue of the head of the organ. *c.t.*, connective tissue of its stalk. × 380.

FIG. 6. The figure represents the tortuous course of the non-medullate fibres (at least, as seen in preparations) of the cochlear nerve across the interspace between the habenula perforata and the hair cells. From the Pig. × 1065.

FIG. 7. Surface view of the epithelium of Reissner's membrane in the Pig. The nuclei of the middle layer of cells shows through the outlines of the inner layer. × 440. Methyl blue.



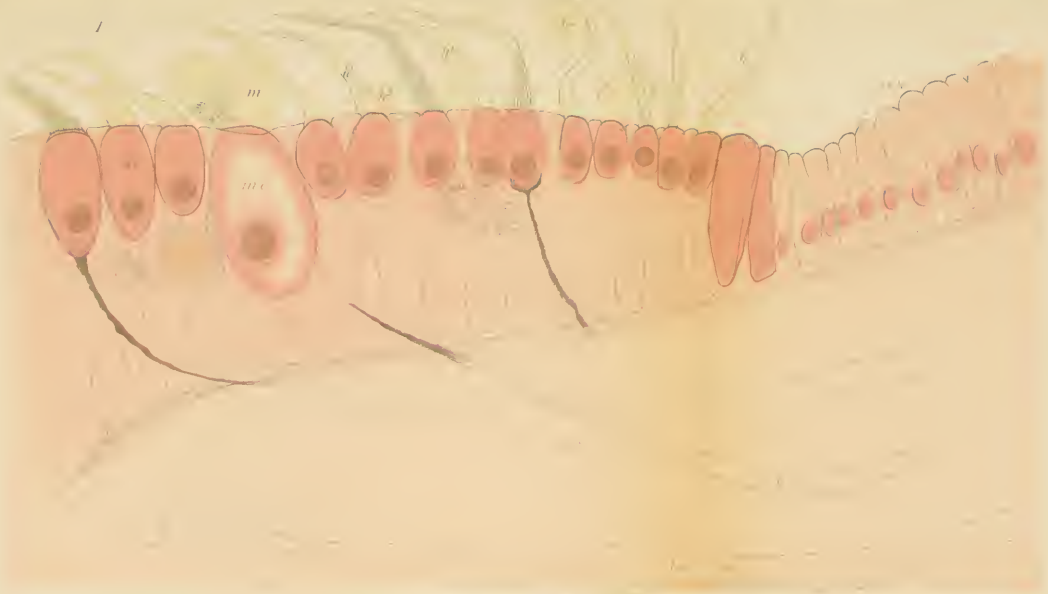
EXPLANATION OF PLATE XI.

FIG. 1. A part of a vertical section of the crista acustica of the Cat's ear. × 1400. To show the effect of reagents on the hairs, and the course of the nerves and the blood-vessels. The very large cupula terminalis is not drawn in. *g.s.*, varicosity of nerve fibre, *n.* *b.v.* and *b.c.*, blood-vessel and contained corpuscles. *m.c.*, mucous cell. *m.*, mucus exuded therefrom. *h.*, $h.^1$, $h.^2$, various forms of hair cells, — remnants. *ep.*, non-sensory epithelium.

FIG. 2. A vertical section of the membrana tectoria, or hair band, of the Virginia Opossum. × 895. *o.h.e.c.*, cell cap of outer hair cell, with its hairs rising into the mass of the band. The entire absence of a "Rand Körper" is noteworthy. *c.p.*, Corti's pillars. *o.h.c.*, body of outer hair cells, not drawn in detail.

FIG. 3. A bundle of lagenar hairs of the Alligator, to show the relation of the otoliths to the hairs. Hrtnk., *ob.* 8, *oc.* 2. Methyl blue.

FIG. 4. A cap of a hair cell from the cochlear organ of the Alligator. × 1400.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mc

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EXPLANATION OF PLATE XII.

FIG. 1. A view in perspective of a portion of the mammalian cochlear organ — organ of Corti. The details are those of the human and Rabbit ears. The figures of the preceding plates render explanatory letters unnecessary.

The hair cells are seen in various conditions, those in the section having their histological detail sketched in. The hair filaments are represented in some of the more important and usual conditions. Their normal relation to the sense cells is shown by the last row of hair cells. Many minor details of cochlear anatomy are left out to secure clearness of the picture, which is true to nature as far as it goes, and disputed points which have no definite and positive solution in my investigations are not introduced. × about 1500.

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MORPHOLOGY.

THE CELL-LINEAGE OF NEREIS.

A CONTRIBUTION TO THE CYTOGENY OF THE ANNELID BODY.

EDMUND B. WILSON.

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THE following studies were undertaken, in the first instance, in the hope of clearing up certain perplexing problems involved in the origin of the germ-layers in annelids, especially those relating to the formation of the mesoblast in the polychætous forms; and, with this end in view, I sought to find a form in which the detailed history of the mesoblast might be followed in the cleavage-process, and its precise relation to the other layers thus determined. For a long time the search was fruitless. The eggs of most of the available American forms proved unfavorable for my purpose, on account of their opacity, the difficulty of orienting the early stages of development, and the lack of distinctive characters in the external features of the blastomeres. At length, however, my attention was directed to the eggs of two species of *Nereis* (*N. limbata*, Ehlers, and *N. megalops*, Verrill), which soon proved to be of unusual interest and importance, not only for the investigation of the mesoblast-formation, but also for the study of the cleavage of the ovum from a more general point of view. In both forms the mesoblast-bands could be traced back to a single cell and the relation of this cell to the other blastomeres accurately determined. The facts thus established, as I have endeavored to show in a preliminary paper (No. 30), go far to reconcile the various modes of mesoblast-formation in annelids, and, as I believe, throw a new light on the well-known researches of Salensky (No. 21) and Kleinenberg (No. 14) in this field. It soon appeared, moreover, that the early stages of *Nereis* possessed a more general interest. The ova are extraordinarily favorable for a detailed investigation of the history of the individual blastomeres in the cleavage-process. They are

transparent and of a convenient size; the differentiation of the blastomeres appears at a very early period; and from the beginning of its development the embryo possesses a number of peculiar features, by means of which it may at any stage be perfectly oriented, almost at a glance.[1] Furthermore, the eggs may easily be fixed and stained by a simple method, which shows with great clearness both the cell-outlines and the nuclear figures. This combination of favorable characteristics renders it possible to trace out the cellular genesis of various parts of the body, step by step from the beginning of development, with a completeness and precision that is rarely attainable. The results show, as I am convinced, that much is to be gained by considering the embryological development of animals from a point of view differing in some respects from that usually adopted, and this point of view I wish to make clear before proceeding to a detailed description of the facts to be set forth.

For many years (more especially since the publication of Haeckel's celebrated papers on the gastræa theory) embryological research has been dominated by certain general conceptions, usually designated as the "germ-layer theory," a term which need not be more precisely defined here. The germ-layer theory forms, in fact, the foundation on which the entire science of comparative embryology is built. And yet it does not require a very extensive search among the embryological writings of the last decade to discover that a surprising divergence of opinion exists among the best authorities in regard to some of the most fundamental propositions of this theory. This divergence need not here be reviewed *in extenso*, but I may be allowed to illustrate its character by quoting somewhat fully from two eminent embryologists. Ten years ago, Balfour wrote as follows:[2] —

"Since there are some Metozoa with only two germinal layers, and other Metozoa with three, and since . . . the third layer or mesoblast can only be regarded as a derivative of one or both the primary layers, it is clear that a complete homology between the two primary germinal layers does not exist.

[1] Dr. E. A. Andrews first called my attention to the favorable character of the *Nereis* eggs and the ease with which they may be procured in large numbers, and I am glad to acknowledge my great indebtedness to him.

[2] *Comparative Embryology*, Vol. II, 1881.

"That there is a general homology appears, on the other hand, hardly open to doubt" (p. 285).

"The fact of the triploblastic condition being later than the diploblastic proves in a conclusive way that the mesoblast is a derivative of one or both the primary layers. . . .

". . . The mesoblast did not at first originate as a mass of independent cells between the two primary layers, but . . . in the first instance it gradually arose as differentiations of the two layers, and . . . its condition in the embryo as an independent layer of undifferentiated cells is a secondary condition, brought about by the general tendency towards a simplification of development, and a retardation of histological differentiation" (p. 286).

Certain facts, clearly specified by Balfour, point, in his opinion, to the establishment of the two following propositions: —

"(1) That with the differentiation of the mesoblast as a distinct layer by the process already explained, the two primary layers lost for the most part the capacity they primitively possessed of giving rise to muscular and connective-tissue differentiations, to the epithelium of the excretory organs, and to generative cells. (2) That the mesoblast throughout the triploblastic Metozoa, in so far as these forms have sprung from a common triploblastic ancestor, is an homologous structure" (p. 287).

The point in this lucid and forcible statement to which I wish to call attention is that *Balfour did not regard the primary germ-layers as being strictly homologous with one another throughout the gastrulas of the triploblastica, or with the layers of the cœlenterate body.* The reasons given for this conclusion are so convincing as to amount almost to a demonstration.

We turn now to the views of Kleinenberg as developed five years later in the celebrated work on *Lopadorhynchus.* In certain respects, as Kleinenberg himself points out, his views coincide with those of Balfour. But when carefully examined as a whole they are found to lead logically to a conception that is diametrically opposed to that of Balfour, as may clearly be shown by a juxtaposition of the two views. It should be borne in mind, however, that it is difficult to give an adequate idea of Kleinenberg's views by the citation of a few passages, since they are set forth in a style which, though always entertaining

from a literary point of view, makes considerable demands upon the patience of the scientific reader. I believe, however, that the gist of the matter lies in the following passages, which follow directly after a very clear review of Balfour's views (the italics are mine): "Die ausgebildeten Cölenteraten besitzen kein Mesoderm und demgemäss erscheint auch das mittlere Keimblatt der Embryonen höherer Metazoen als ein bloss conventioneller, den Thatsachen nicht entsprechender, Begriff. Was man bisher so nannte ist entweder die Summe unabhängiger heterogener Anlagen, die im Bereich der primären Keimblätter entstehen, oder eine einzige Anlage eines bestimmten Gewebes oder Organs, die eventuell theilweiser Umbildung unterliegt. Am häufigsten sind mächtige ektodermale Muskelanlagen und paarige Anhänge des Urdarms zum mittleren Keimblatt gemacht worden. Die Frage nach der Homologie des sogenannten Mesoblasts in den verschiedenen Thierklassen beruht auf der Voraussetzung des Vorhandenseins eines Nichtvorhanden, und fällt daher von selbst weg. *Die Homologie der Organe muss in jedem Falle, mit Berücksichtigung etwaiger Substitutionem, durch die genetischen Beziehungen zu den beiden Blättern des Cölenteratenkörpers festgestellt werden. Ektoderm und Entoderm sind die ursprünglichen Grundlagen aller Gewebe und Organe — die Geschlechtszellen wahrscheinlich ausgenommen — bei den Cölenteraten: ebenso verhält sich das Ektoderm und das Entoderm der Entwicklungsformen.* Diese Blätter erzeugen besondere Gewebe ohne dadurch irgend wie die Fähigkeit neuer Gewebebildung einzubüssen (p. 18).

It would be manifestly unfair to take this passage as an adequate statement of Kleinenberg's views. But it leaves no doubt as to his conception of homologies. They are equivalent phylogenetic relationships to the layers of the cœlenterate body. It seems equally clear, furthermore, that he believes *these phylogenetic relationships to be repeated or expressed by corresponding equivalent ontogenetic relationships to the primary germ-layers of the gastrula.* Here is the key to Kleinenberg's whole position, for it obviously rests upon the assumption that the two primary germ-layers — the inner and outer layers of the gastrula — are respectively homologous with the layers of the cœlenterate body, and hence with each other throughout the Triploblastica. The two-layered gastrula is a strictly ancestral

larval form — and this, as I believe and shall endeavor to show further on, is an unwarrantable assumption which ultimately leads to the most contradictory and perplexing results. That this is really Kleinenberg's meaning is, I think, proved by his reasoning throughout the entire paper. It is strikingly illustrated, for example, in his treatment of the annelid trochophore (p. 176). After pointing out certain so-called homologies between the organs of the trochophore (ring-nerve, ring-muscle, ciliated belt) and those of a medusa (ring-nerve, ring-muscle, velum or umbrella-margin), he says : —

"Giebt man diese Homologien zu, so würde man ein fertiges geschlechtsreifes Thier von der Organisation der Lopadorhynchuslarve im System gewiss entweder in die Ordnung der Hydromedusen einstellen oder wenigstens am nächsten zu diesen setzen. Die Principien der Klassifikation müssen aber dieselben bleiben, ob es sich um die Endstadien oder um die Zwischenstadien eines Evolutionscyclus handelt, und wenn ich in der Entwicklung eines Annelids eine Form finde, die von der Annelidenorganisation gar nichts besitzt, dagegen in den wesentlichsten Theilen einer Meduse gleichartig ist, so nehme ich sie auch nicht für ein Annelid sondern für eine Medusa."

In passing I may remark that such "principles of classification" lead to a complete *reductio ad absurdum* when applied to the earlier stages of development (see p. 441). Here, however, I call especial attention to the fact that the passage is devoid of meaning, either in itself or in connection with those already quoted, except under the fundamental assumption that the inner and outer layers of the larva (and of the gastrula) are respectively homologous with those of the cœlenterate body.

It appears, therefore, broadly speaking, that Balfour and Kleinenberg reason in precisely opposite directions, the premises of either being the conclusions of the other. Balfour, assuming the homology of the mesoblast (with certain reservations that do not affect the general result) is logically compelled to deny the precise homology of the ectoblast and entoblast. Kleinenberg, on the other hand, assumes the homology of the primary layers, and is then led over the same path, but in the reverse direction, to the conclusion that the mesoblast is not homologous. Kleinenberg takes the gastrula as a primary or ancestral larval form ; while Balfour, if I understand him cor-

rectly, regards it as *moulded* upon the Cœlenterate type, but modified by secondary changes involved in the differentiation of the mesoblast as a distinct germ-layer.

In what direction may we seek to break away from this deadlock of opinion? It appears to me that the only course open to embryological investigation is to examine more precisely the origin of the gastrula itself; *to take as a starting-point not the two-layered gastrula, but the ovum.* The "gastrula" cannot be taken as a starting-point for the investigation of comparative organogeny unless we are certain that the two layers are everywhere homologous. Simply to assume this homology is simply to beg the question. *The relationship of the inner and outer layers in the various forms of gastrulas must be investigated not only by determining their relationship to the adult body, but also by tracing out the cell-lineage or cytogeny of the individual blastomeres from the beginning of development;* and I am convinced that many apparent contradictions that appear under the ordinary germ-layer theory will disappear when thus examined.

It is from this point of view that I have considered the development of *Nereis*. It will be shown that many important organs and systems of the annelid body can be traced back to parent blastomeres — I propose to call them *protoblasts* ("Ur-zellen") — that are differentiated long before the completion of the "gastrula" stage, and whose relations to one another can be determined with all possible accuracy. The development in fact suggests a mosaic (to use a comparison of Roux's); the ontogeny may be resolved into a series of individual organogenies, each of which takes its beginning in a single protoblast or a small group of them. I shall endeavor, therefore, first to determine the origin and mutual relationships of the individual protoblasts in the cleavage process, and, second, to trace their later history. The relation of the protoblasts to the germ-layers of the gastrula becomes afterwards a simple question.

It remains to be seen whether this method of study will be found sufficiently practicable in other animals to afford a satisfactory basis of comparison, and to what conclusions it may lead, but some interesting results have already been attained in this direction. These researches need not be fully reviewed at this point, but I must refer briefly to Whitman's epoch-making researches on the Hirudinea,[1] which not only opened a new

[1] Nos. 27, 28.

field in the study of annelid embryology, but, as I believe, formed a new point of departure for a re-examination of the entire germ-layer theory. Whitman showed (in *Clepsine*) that the entire germ-bands of the trunk could be traced back to five pairs of cells (teloblasts), whose origin in the cleavage was accurately determined. One pair (primary mesoblasts) gave rise to the mesoblast-bands; one pair (neuroblasts) to the ventral nerve-cord; two pairs ("nephroblasts") to the trunk-nephridia, and one pair (lateral teloblasts), as he conjectured, were perhaps concerned in the origin of the muscles. That an entire system of organs, such as the ventral nerve-cord, or the trunk-nephridia could be traced back to a single blastomere was a fact so extraordinary that many morphologists, Balfour among them, at first refused to credit Whitman's statements, notwithstanding the fact that the origin of the entire mesoblast from a single cell had been established in a number of cases. Later investigation, however, not only confirmed Whitman's discoveries, but extended them to other Hirudinea and to the Oligochæta; and the fact that the special interpretation placed by him upon the "nephroblasts" has been disputed does not lessen the importance and significance of the work. Whitman's researches showed that the material for complicated adult organs might be so condensed and accelerated in development as to be set apart by a single stroke, as it were, in the early stages of cleavage, long before the establishment of the gastrula; and this fact opens up a long vista of possibilities regarding the secondary modification of the gastrula stage. It may be urged that these modifications can have little general interest for the very reason that they are secondary and take place only in a highly modified type of development. The reply to this is, how do we know what is the primitive type of gastrulation? The present state of embryology certainly does not enable us to give any positive answer to this question. Whether the primary form is the epibolic or the embolic gastrula, the plakula, the unipolar or multipolar delaminate planula, or a still different type, remains to be seen; and the very fact that the differentiation of the layers is effected in such a diversity of ways proves conclusively that these early stages of development are as susceptible to secondary modification as the later. I shall show, further on, that the history of the mesoblast in *Nereis* shows how a slight

change in the character of the segmentation in one direction or another would cause the mesoblast to take its apparent origin in the one case from the entoblast, in the other from the ectoblast. Supposing these divergent changes to take place in two originally similar forms — there is every reason to believe that exactly analogous changes have taken place — would the two resulting forms of "gastrulas" be equivalent? Is the two-layered larva of *Amphioxus* equivalent to that of *Lopadorhynchus?* I think not.[1]

The development of *Nereis* has been investigated, especially by Götte (No. 9), Salensky (No. 21), myself (No. 30), and v. Wistinghausen (No. 31). Götte describes, in *N. Dumerilii*, the cleavage, the general features of the gastrulation, the origin of the mesoblast from a single cell (which, however, has probably nothing to do with the mesoblast), and the general history of the free-swimming trochophore.

Salensky did not observe the early stages of cleavage, but accurately figured some of the later stages and made an admirable study of the early larva by means of actual sections. His results differ from those of Götte on two points of fundamental importance, of which the first relates to the mesoblast-formation, the second to the axial relations of the larva. (1) Götte describes the mesoblast as arising from a single cell (produced immediately after the eight-celled stage), which, after dividing into two, passes into the cleavage-cavity and gives rise to the mesoblast-bands, precisely as in the Oligochæta and Hirudinea. According to Salensky, on the other hand, the mesoblast is formed by a proliferation of the ventral ectoblast near the lip of the blastopore (*loc. cit.* p. 568). (2) As to the axial relations, Götte describes and figures the mesoblast-bands in their earlier stages as lying horizontally (*i.e.* parallel to the prototroch), so that the antero-posterior axis as thus determined is likewise horizontal. Salen-

[1] In a recent interesting paper (No. 26) Watase has called attention to the importance of the precise examination of the early stages of cleavage by tracing the cell-lineage. I am fully in agreement with the views there set forth, though I cannot fully accept his general conclusions (*cf.* p. 455), and it appears to me that the relation between this "cytological method" and the study of the germ-layers is not very clearly explained. The phrase "cytological method" is open to some objection, since in common usage the word *cytology* is applied to the study rather of the internal phenomena of the cell than of its external relations. The terms *cytogeny*, *cytogenetic* seem to me more suitable, though perhaps open to criticism on other grounds.

sky finds, on the other hand, that the mesoblast-bands are from the first perpendicular to the prototroch, — *i.e.* at right angles to the position described by Götte.

My own results, briefly set forth in the paper referred to, differ totally from those of Götte and agree essentially with the *facts* described by Salensky, though a study of the early stages leads to a very different interpretation. (1) I showed that the mesoblast arises from a single cell, the "second proteloblast" (by no means, however, the cell described by Götte), the offspring of which give rise to a V-shaped mass of cells, the two arms of which form the mesoblast-bands. These bands have in every respect the same position and relations as described by Salensky. The apex of the V extends to the surface at the posterior lip of the blastopore, so that the mesoblast-bands apparently take origin in the ectoblast, as Salensky states. The primary mesoblast-cell itself arises in a characteristic manner from the large, left posterior macromere, precisely as in *Clepsine*, *Rhynchelmis*, and in the gasteropod *Crepidula*, recently described by Conklin (No. 4).[1] (2) At the fourth cleavage a large cell, the "first proteloblast," separates from that macromere which afterwards gives rise to the mesoblast. From this cell (which is evidently identical with the primary mesoblast of Götte) arises the entire ventral plate of the trochophore, — *i.e.* the ventral neural plates, the seta-sacs, and probably a portion of the nephridia.

These results were published in a condensed form, in connection with the discussion of other questions, as I was still engaged in the investigation of other features of the ontogeny. The paper of v. Wistinghausen appeared soon afterwards, and his results were independently attained, although my paper had been received before their publication.[2] The species investigated was the "Nereis-form" of *N. Dumerilii* (the same as Götte's species), which lays its eggs in tubes and has a suppressed trochophore, whereas Götte's studies were based upon the "Heteronereis-form," which has pelagic eggs and a free-swimming trochophore. The results confirm my own on every essen-

[1] Through the kindness of Professor Conklin, I have been enabled to examine many of his drawings and preparations in advance of the publication of the full paper.

[2] It may be added that the investigations described in the present paper were practically finished before the appearance of v. Wistinghausen's paper.

tial point. The origin and fate of the two "proteloblasts" (called "somatoblasts" by v. Wistinghausen) are the same, and so are the orientation and general history of the germ-bands, though there are certain interesting differences of detail. His orientation of the first three cleavage-planes also agrees exactly with mine, though his terminology is different, owing to a different designation of the trochophore-axes. A more extended review of his results will be given further on.

A comparison of these investigations leaves no room to doubt that Götte's orientation of the mesoblast-bands and his account of the first origin of the mesoblast are both erroneous. It is barely possible that the free-swimming trochophores of *N. Dumerilii* differ from the suppressed trochophores in regard to the early development, but this is extremely improbable in view of the fact that the suppressed trochophores agree precisely with the free-swimming trochophores of three other species (*N. limbata*, *N. megalops*, and *N. cultrifera*). I venture to assert that a comparison of Götte's figures with those given in the present paper will leave no room to doubt that the cells described by him as "primary mesoblasts" are the posterior proteloblasts (*i.e.* the first progeny of the first somatoblast, p. 407), viewed obliquely in optical section, and that the real primary mesoblasts are figured by him as ordinary ectoblast-cells at the posterior lip of the blastopore. His figures of the horizontal mesoblast-bands I will not undertake to explain.

In the present paper I shall consider mainly the external aspects of the cleavage and the general relations of the larval and adult bodies. I have devoted my attention mainly to surface views, partly because this part of the subject has hitherto been least known and has proved most fruitful of new results, partly because this part of the work demanded so great an expenditure of time and labor that I have been forced to defer to a later paper an account of the internal phenomena of cleavage and a detailed study of the differentiation of the tissues and organs.

Egg-laying. — Methods.

The eggs of *N. limbata* and *N. megalops* are discharged at night while the animals are actively swimming at the surface of the water. At Wood's Holl, Mass., the season extends at least

from June to September, the most favorable time, as far as I have been able to determine, being in August and the earlier part of September. The animals appear in abundance only on warm, still nights, and even then are rarely found unless the water has been quiet for some days. When the conditions are favorable, they come forth soon after dark and swim rapidly about at the surface, sometimes in almost incredible numbers. There is something capricious about their occurrence, and I have never been able to find a satisfactory explanation of their vagaries. Sometimes both species occur together; at other times, under apparently similar conditions, only one species will be found, or one may be very abundant and the other rare. The sexes are, as a rule, readily distinguishable, since the males are bright red and swim very rapidly, while the females are paler in color (often nearly white) and swim slowly. The males are always more abundant than the females, and I have sometimes captured thousands of males without finding a single female. The females are often actively pursued by the males, and have a habit of swimming in a circle, closely pressed by numerous males, while the eggs and spermatozoa are being discharged into the water.

The best method of procedure is to capture the adults singly with a hand-net by the light of a lantern, which serves to attract the animals, and by means of which they can be distinctly seen. The sexes should be carefully separated, since otherwise the eggs are immediately fertilized and are so thickly covered with spermatozoa that it is afterwards difficult to study them. As soon as one or two ripe males are placed with the females, the eggs and spermatozoa are discharged. The animals should then be as quickly as possible removed (so as to allow the eggs to sink), and the water thereupon repeatedly changed until all superfluous spermatozoa are removed. If the sexes are kept apart, the eggs are as a rule not discharged, and I have often endeavored to keep the animals until morning, so as to study the development by daylight. Unfortunately, however, the animals usually die when thus treated, and even if the eggs are deposited and fertilized (either naturally or artificially) on the following day, they do not develop normally. Artificial fertilization is easily effected at night, and my best material has been obtained in this way, since a minimal quantity of spermatozoa is

thus ensured. Most of the eggs I have studied were deposited about 9 P.M., but in a few cases they were not laid until an hour or two later. The cleavage was repeatedly followed through the entire night on the living ova, and most of the cleavage-stages have been observed scores of times. Owing to the warmth of the lamp, the eggs develop more rapidly under the microscope than in the aquarium, so that, by keeping the aquarium cool and taking fresh material after the completion of each division, every step in the cleavage may be observed twice or more in the same lot of eggs.

I have found it best to examine the eggs on an ordinary glass slide under a very long narrow cover-glass, one end of which is supported by wax feet. The eggs are drawn up in a pipette and run under the cover-glass from the upper end, whereupon they arrange themselves in a single layer. By moving the cover-glass the eggs may be rolled, though with some difficulty owing to the presence of oil-drops which cause the eggs to lie with the animal pole downwards. In later stages, after the larvæ begin to swim, they may be paralyzed by adding to the water a few drops of a weak solution of cocaine in dilute methyl alcohol. The cilia may thus be brought to a standstill and their arrangement easily studied. The embryos may also be colored *intra vitam* to any desired extent by adding a one per cent aqueous solution of methyl-blue to the water. This method does not give a differential staining, but is very useful in certain stages by rendering the protoplasm and cell-outlines more distinctly visible.

For preserving the embryos various methods were employed. For sections the best hardening fluids are Flemming's fluid (Fol's weaker formula), Perenyi's fluid, sublimate, and chrom-acetic acid, especially the two former. Kleinenberg's picric acid, which gives beautiful results with many annelid larvæ, and which was successfully employed by v. Wistinghausen for *N. Dumerilii*, I have found unsatisfactory. It is, furthermore, a curious and instructive fact that Lang's sublimate acetic mixture, which v. Wistinghausen found useless, works very well with the American species. These reagents were employed in the usual manner, the eggs being left in them from ten to thirty minutes.

These methods are, however, of small value in comparison

with that employed for the surface-views and optical sections, and to it I owe many important results. This is simply strong acetic acid mixed in various proportions with glycerine and water. I have usually employed a mixture of glycerine, glacial acetic acid, and water in equal parts (a modification of "Haller's fluid," suggested to me by Dr. Watase). The eggs are placed directly in this fluid and kept there until needed, *i.e.* for an indefinite period. They are perfectly fixed, without change of form, and undergo no deterioration for several weeks except a gradually increasing vacuolation of the protoplasm. For examination they are stained as follows. A number of the eggs, *still lying in the fluid*, are transferred with a pipette to a watch-glass and a few drops of Schneider's acetic carmine (saturated solution of carmine in forty-five per cent acetic acid) are added. The proper degree of staining must be determined by examination; the time required depends upon the amount of carmine added. The color should be *light* red, and I have usually found three to five minutes sufficient with a rather weak carmine. The embryos are then washed *by repeatedly changing the glycerine-acetic* fluid until all superfluous color is removed; they are then mounted, still in the fluid, under a long cover-glass as usual. They may be examined immediately, but the embryos become far more transparent if the preparation be set aside for several hours until the water evaporates, *e.g.* over night. (After a day or two the color begins to alter and to darken, and the preparation soon becomes useless.) If, now, a favorable specimen be selected, slightly compressed and carefully rolled about from side to side by displacing the cover-glass with a needle, the cells may gradually be caused to separate from one another. If the process be stopped at precisely the right point, when the cells have barely begun to separate, preparations of the utmost beauty and clearness may be obtained. The protoplasm is colored pale red, the resting nuclei and the karyokinetic figures show with perfect distinctness, and especially the cell-outlines are shown with diagrammatic clearness. In good preparations, even of comparatively late stages, every cell in the embryo may be seen and the relations of the dividing cells studied with the utmost accuracy. Most of the figures have been drawn from specimens prepared by this method, and to it is owing the relative completeness with which I have been able to study the cleavage-

process. Unfortunately the preparations cannot be kept permanently. Fairly good permanent preparations may be made by mounting (in balsam or glycerine) specimens hardened in Flemming's or Perenyi's fluid and stained with hæmatoxylin or alum cochineal; but they are not to be compared with the others. Specimens preserved in Perenyi's fluid are apt to darken in time, possibly through the action of the tannin dissolved by the alcohol when cork stoppers are used. Such specimens often make very good preparations when mounted in balsam without staining.

I. The Unsegmented Egg.

The eggs are discharged separately into the water and soon sink to the bottom, where they lie with the animal pole turned downward. Each egg is surrounded by a transparent, thick, gelatinous envelope, which causes the eggs, when in masses, to be separated by considerable spaces. Occasionally the envelopes of a number of eggs adhere closely together, so that the eggs appear as if imbedded in a common jelly, as is regularly the case with *N. cultrifera*, and some other species; this, however, is exceptional, and, as a rule, the eggs move freely amongst one another. To the periphery of the gelatinous envelope the spermatozoa adhere in great numbers, so that the eggs appear to be surrounded by a kind of halo, which, if the water is not changed, soon becomes so dense as to obscure the vitellus within it.

The vitellus is transparent, finely granular, and contains (in *N. limbata*) at least three kinds of elements besides the protoplasm. These are (1) large oil-drops, (2) small oil-drops, and (3) deutoplasm-spheres. The latter are not present in the eggs of *N. megalops*, or, if present, are invisible, owing to their transparency. The large oil-drops, which vary in number from ten or twelve to twenty or more, and also vary greatly in size, are arranged in an irregular circle (Figs. 1, 2) near the periphery of the vitellus in the lower (vegetative) half of the egg, which is thereby caused to lie with this pole turned upwards. If the egg be turned over, it soon rotates back into its original position, so that it is difficult to follow continuously the history of the upper hemisphere in the living egg. The small oil-drops (Fig. 1) are very minute, highly refractive spheres

scattered at rather wide intervals through the entire vitellus. I am unable to say whether they are of the same nature as the large drops, but intermediate forms seem not to exist. The deutoplasm-spheres (Fig. 1) are intermediate in size between the two forms of oil-drops. They are at first equally distributed through the vitellus, and only after fertilization do they begin to disappear from the upper pole (as will be described further on). In appearance they are clear and homogeneous, approximately spherical, but with rather irregular outlines, more highly refractive than the protoplasm, but much less so than the oil-drops.

When first discharged, the eggs are somewhat irregular in form. Soon, however, they become perfectly spherical with a diameter of about 0.12 to 0.14 mm. in *N. limbata*, considerably less in *N. megalops* (the eggs of both species vary considerably in size). The vitellus is at first surrounded by two membranes, the outer of which is extremely thin and delicate, the inner (*zona radiata*) much thicker and with very distinct radial striations. I shall not attempt in this place to give any account of the internal phenomena of fertilization, but there are certain peculiar external phenomena to which it may be useful to call attention. From twenty to thirty minutes after fertilization the striæ of the zona suddenly become indistinct, and in the course of two or three minutes the zona itself entirely disappears, leaving only the outer membrane. The vitellus meanwhile becomes irregular in form, and after the disappearance of the zona, assumes an amœboid appearance, so as to be here and there widely separated from the membrane. For about ten minutes slow amœboid changes of form take place, after which the vitellus again becomes perfectly spherical, but is separated from the outer membrane by a slight space. Meanwhile certain changes, preparatory to the extrusion of the polar cells, take place at the upper pole.

The freshly laid egg has a large germinal vesicle which lies excentrically, somewhat above the centre of the vitellus; a few minutes after fertilization the vesicle disappears. Towards the close of the amœboid phase the deutoplasm-spheres begin to migrate away from the upper pole, leaving a clear polar area composed of granular protoplasm. In it may be seen a few scattered oil-drops of the small form, but deutoplasm-spheres

are wholly absent. The polar area slowly increases in size until its diameter is about one-third that of the vitellus, and meanwhile a very distinct star appears in its centre. Thirty-five to forty minutes after fertilization the first polar cell is extruded, and the second follows ten or twelve minutes later. Viewed from the side at this period (Fig. 2) the vitellus appears somewhat flattened on the upper hemisphere and is separated from the membrane by a considerable space. I would call attention to the fact that the polar cells differ slightly both in size and in form, the first being pear-shaped or oval, while the second is spherical and somewhat smaller. The corresponding internal differences have not yet been investigated.

II. General Sketch of the Development.

The cleavage of the ovum takes place with a precision and regularity which oft-repeated examination only renders more striking and wonderful. Up to a stage when the foundations of all the more important organs have been established (sixty-two cells or more) the divisions take place with clock-like regularity, the only perceptible variations being slight differences in the time at which the individual blastomeres divide. Even these differences are so slight as to escape any but the closest scrutiny. As development proceeds the variations become more marked, and thus individual differences between the embryos gradually become apparent. Yet these differences, as before, are for the most part the result of slight time-variations in the development of individual blastomeres and their progeny, and, as far as can be determined, do not materially affect the end result. The entire ontogeny gives the impression of a strictly ordered and predetermined series of events, in which every cell-division plays a definite *rôle* and has a fixed relation to all that precedes and follows it.

The events of the cleavage fall into three very marked periods which I shall designate respectively as the (1) spiral, (2) transitional, and (3) bilateral periods. In the first period, which extends to the thirty-eight-celled stage, the germ-layers are completely differentiated. At the same time most of the individual blastomeres are differentiated into the parent-cells or protoblasts from which the future organs arise. The embryological

material is, as it were, sifted out and arranged; but it is a very remarkable and interesting fact that the cell-divisions by which this is effected do not take place bilaterally in accordance with the adult structure, but show a peculiar modification of radial symmetry which is best characterized as spiral in character, and *which cannot be reduced to the bilateral type.*

The cleavage is total and unequal; no cleavage cavity is formed, the gastrulation is strictly epibolic, and the "blastopore" closes at a point that nearly coincides with the lower pole, *i.e.* 180° from the point at which the polar cells are formed. The first cleavage is transverse to the median plane of the trochophore and at right angles to the plane of the prototroch, hence horizontal with respect to the adult body, owing to a peculiar shifting of the axes, which will be described in the course of the paper. The second cleavage-plane ultimately coincides with the median plane of the trochophore and of the adult body, *though it does not divide the egg into equal halves.* The third cleavage-plane is as usual horizontal or equatorial (parallel to the prototroch) and separates four smaller micromeres above from four macromeres below.

Three sets of four "micromeres" each are successively separated from the macromeres (*A*, *B*, *C*, *D*, Diagram 1) by the following invariable law. The first four (a^1, b^1, c^1, d^1) are formed in a right-handed spiral, the second four (a^2, b^2, c^2, d^2) in a left-handed spiral, and the third set (a^3, b^3, c^3, d^3) in a right-handed spiral like the first set. (I follow Lang's terminology, as applied to the ovum of the polyclade, *Discocœlis*, with which the segmentation of *Nereis* accurately agrees up to a late stage.) From these twelve micromeres the entire ectoblast arises. Their formation is followed by the separation of the primary mesoblast, or "second somatoblast" (d^4 or *M*) from the left posterior macromere, with which event the differentiation of the germ-layers is completed and the strictly spiral period ends. The micromere d^2 or *X*, which is much larger than the

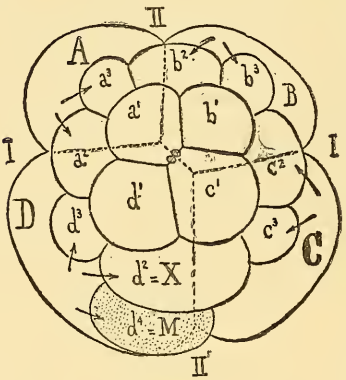


Diagram I.

others, is the "first somatoblast," and from it arises the ventral plate.[1]

The spiral character of the cleavage is strictly maintained in the divisions of the micromeres which meanwhile take place. At the close of the period (Fig. 29) the embryo consists of thirty-eight cells, the relations of which to the germ-layers are as follows: —

4 Macromeres		= Entoblast.
34 Micromeres	33 Ectomeres	= Ectoblast.
	1 Mesomere	= Mesoblast.

Bilateral divisions now begin to appear among some of the ectomeres, but others still continue to divide spirally; *i.e.* the bilateral period is overlapped to some extent by the spiral. This period of overlapping, in which the number of cells increases from thirty-eight to fifty-eight (Figs. 30 to 38), I shall call the Transitional Period. Its principal event is the establishment of the prototrochal girdle and of a remarkable cross of cells on the upper hemisphere which gives rise in part to the cerebral ganglia.

In the third, or Bilateral Period, the divisions become essentially bilateral, and so remain as long as they can be followed. The embryo is still perfectly spherical, and its cells are not arranged according to a strict bilaterality, because they still show traces of their spiral mode of origin. Little by little, however, a complete bilaterality is established, which becomes very apparent as soon as the elongation of the body begins to take place.

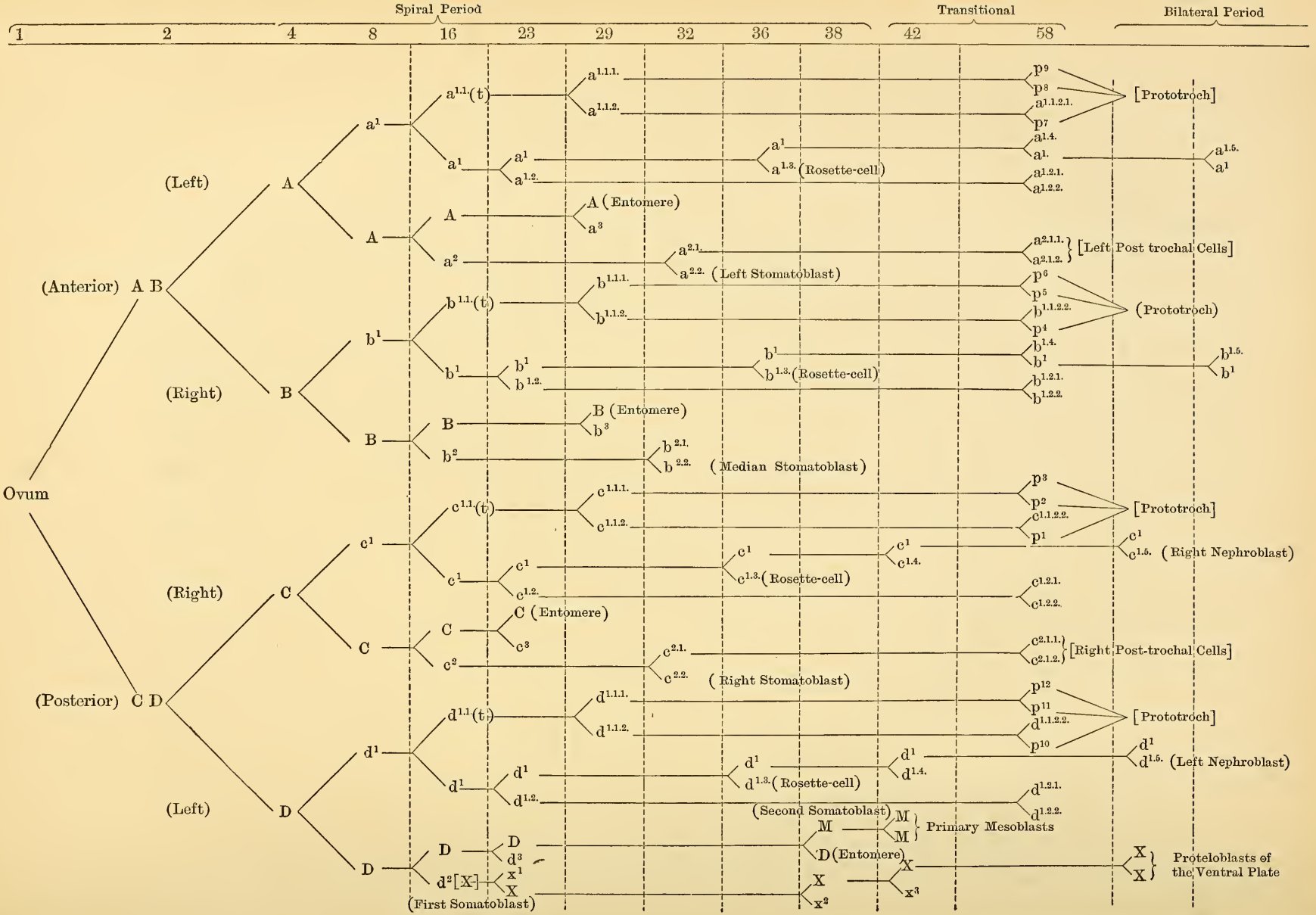
The young trochophore (Fig. 82) is nearly spherical in form. The prototroch occupies the equatorial plane, and is composed of a girdle of twelve principal cells (derived from products of the first set of micromeres). The girdle is interrupted in the median posterior (*i.e.* dorsal) line by a narrow space through which the small cells of the upper hemisphere are in continuity with those of the lower. In the centre of the upper hemisphere, at the point where the polar cells were formed, is an apical tuft of cilia. Two eye-spots are symmetrically placed on the upper hemisphere. The mouth, which opens into a large

[1] I shall adopt v. Wistinghausen's term "somatoblast" in place of the word "proteloblast" employed in my earlier paper, reserving the latter term for a different use (p. 407).

stomodæum, is in the median ventral line posterior to the prototroch. The anus is not yet formed, but its future position is indicated by a pigmented area that lies nearly in the centre of the lower hemisphere. At this point, as will be shown further on, the blastopore has closed, and here the mesoblast-bands reach the surface. The subsequent elongation of the body (Pl. XX) takes place in the vertical axis of the trochophore, which coincides with the principal axis of the ovum.

This preliminary statement will allow the following description to be made more condensed, and, I trust, more intelligible. It may be added that the spiral period of cleavage in *Nereis* is marvellously similar to the cleavage of the polyclade ovum as described especially by Götte, Selenka, and Lang, and shows an equally striking similarity to the cleavage of the molluscan ovum (Bobretzky, Blochmann, Conklin, etc.). It is important to notice, however, that although the *form* of cleavage in the spiral period of *Nereis* is identical with that of the polyclade, yet the corresponding blastomeres are only in part homologous. The significance of this very remarkable fact is discussed further on.[1]

[1] It is absolutely necessary to fix, at the outset, the terms employed in the orientation of the larva, since there is room for a wide difference of opinion which may easily lead to a confusion of terms, and the orientation I shall employ differs radically from that of v. Wistinghausen. I shall regard the principal or vertical axis of the trochophore as representing, *roughly speaking*, the dorso-ventral axis (antero-posterior, v. W.), the prototrochal plane as approximately longitudinal (dorso-ventral, v. W.), the gap in the prototroch as approximately posterior (median-dorsal, v. W.), and the opposite point as anterior (median ventral, v. W.). My orientation agrees essentially with that of Götte and Lang as applied to the polyclade larva, while v. Wistinghausen follows that of Selenka. The difference is essentially this: v. Wistinghausen orients the ovum and the trochophore directly with reference to the adult body, and thus identifies the principal or vertical axis of the ovum with the antero-posterior axis of the adult. I believe, on the other hand, that a shifting of the axes takes place, so that, *broadly speaking*, the larval axes are at right angles to those of the adult. Thus, (1) the posterior extremity, (2) the ventral region, and (3) the anterior region of the embryo and early larva become in v. Wistinghausen's terminology respectively (1) dorsal, (2) posterior, and (3) ventral. I regret this confusion of terminology, since I am perfectly in accord with v. Wistinghausen in regard to the facts. I wish, however, expressly to disclaim any intention of attaching a profound morphological significance to the terminology employed; for, as will be shown hereafter, the axes of the young embryo cannot be very accurately defined. The general axial shifting that takes place in the metamorphosis is, however, not ideal, but real — it is an actual transference of material; and if this shifting is not recognized, the terminology of the early stages becomes in the highest degree confusing and contradictory. My orientation is, therefore, adopted for purely practical reasons, *i.e.* for convenience of description.


Spiral Period
Transitional
Bilateral Period
1
2
4
8
16
23
29
32
36
38
42
58
Ovum
(Anterior) A B
(Posterior) C D
(Left)
(Right)
(Right)
(Left)
A
B
C
D
a¹
b¹
c¹
d¹
a¹·¹·(t)
b¹·¹·(t)
c¹·¹·(t)
d¹·¹·(t)
a¹·¹·¹·
a¹·¹·²·
a¹·¹·²·¹·
a¹·¹·²·²·
a¹·²·
a¹·³·
a¹·⁴·
a¹·⁵·
A (Entomere)
a³
a²
a²·¹·
a²·²·
(Left Stomatoblast)
[Left Post trochal Cells]
b¹·¹·¹·
b¹·¹·²·
b¹·¹·²·²·
b¹·²·
b¹·³·
b¹·⁴·
b¹·⁵·
B (Entomere)
b³
b²
b²·¹·
b²·²·
(Median Stomatoblast)
(Prototroch)
c¹·¹·¹·
c¹·¹·²·
c¹·¹·²·²·
c¹·²·
c¹·³·
c¹·⁴·
c¹·⁵·
(Right Nephroblast)
C (Entomere)
c³
c²
c²·¹·
c²·²·
(Right Stomatoblast)
[Right Post-trochal Cells]
d¹·¹·¹·
d¹·¹·²·
d¹·¹·²·²·
d¹·²·
d¹·³·
d¹·⁴·
d¹·⁵·
(Left Nephroblast)
(First Somatoblast)
d²[X]
x¹
X
(Second Somatoblast)
M
M
Primary Mesoblasts
D (Entomere)
d³
x²
x³
Proteloblasts of the Ventral Plate
[Prototroch]
p¹
p²
p³
p⁴
p⁵
p⁶
p⁷
p⁸
p⁹
p¹⁰
p¹¹
p¹²

A general view of the cleavage may be obtained from the accompanying diagram or cytogenetic tree (p. 382), which represents accurately the genetic relations of the blastomeres up to the complete establishment of bilaterality. The number of blastomeres in the successive stages is given in the upper line; the succession of the divisions is shown by the vertical columns. The record is without a gap up to the fifty-eight-celled stage. Beyond this point the development of the embryo as a whole cannot be fully represented in the diagram, on account of increasing variations in the order of division of the individual cells. Special diagrams showing the history of some of the individual protoblasts will be given further on.

III. Spiral Period of Cleavage

(1 to 38 blastomeres).

1. *The First Cleavage* (Figs. 2^a to 3).

The first cleavage takes place about seventy-five minutes after fertilization. The plane of division passes slightly to one side of the polar cells, and divides the egg into two unequal parts (*AB* and *CD*). The subsequent history shows that the first cleavage plane is vertical and at right angles to the median plane of the larval body, and at right angles to the prototroch. The smaller of the two cells (*AB*) is anterior ("ventral," v. Wistinghausen), the larger (*CD*) is posterior ("dorsal," v. Wistinghausen).

The division is initiated by the appearance of a shallow, transverse furrow on the upper side of the ovum, which gradually deepens and ultimately cuts through the entire vitellus from above downwards. The furrow is so placed as to divide the clear polar area into unequal parts, about one-third of it passing into the smaller cell and two-thirds into the larger. As the furrow travels downwards, a number of interesting phenomena may be observed. The furrow is at first very broad, with widely separated margins, which only approach and come into contact when the furrow has cut about one-third through the vitellus. As they approach, the margins become irregular and put forth amœboid processes, consisting mainly of clear protoplasm, though

occasionally containing a few deutoplasm-spheres. The processes of the opposing margins first come into contact near the middle of the furrow (*i.e.* near the upper pole), and are gradually flattened out against one another, so that the central portion of the furrow becomes a straight, even line. From this initial point of union, the closure of the furrow proceeds in like manner in each direction, around to the opposite side of the vitellus, after which the two blastomeres become pressed together, and the egg enters upon a resting period of fifteen to twenty minutes. The entire cleavage occupies about five minutes.

The behavior of the vitellus during the division gives the impression that the protoplasm is a viscid, tenacious mass, like pitch, which is pulled apart into two masses, against a considerable resistance. When, for example, the furrow has cut nearly through the vitellus, a narrow bridge of protoplasm is often left at the lower pole. As this bridge is cut through, the deutoplasm-spheres within its substance are drawn out into an oval shape, as if the viscid mass were being dragged out by the ends. The formation of the pseudopodial processes shows, however, that the protoplasm is actively at work, and that it is not passively sundered by attractive forces, emanating from a central point within each incipient blastomere. It is worthy of note, furthermore, that the edges of the furrow appear to be pressed together with considerable force, since the pseudopodial processes may be seen to flatten out against each other, as if urged from the rear. While this operation is taking place on the upper portion of the furrow, however, the lower portion is still cutting down through the vitellus, — a fact which likewise has some bearing on the theory of attractive centres. As the cleavage-furrow passes downward, it seems to carry with it the anterior third of the polar area which disappears between the two blastomeres as they flatten together. The remaining two-thirds still persists in the larger blastomere as an irregular, clear space. In this space I have been able to see, in some specimens, but not in all, an irregular, coarsely granular mass, which shows a marked contrast to the surrounding protoplasm, although it has no definite boundary. This mass lies somewhat to the left of the middle line, and at the next cleavage passes into the left posterior macromere (*cf.* Figs. 3 and 5). Its later history I have not followed with sufficient care, but I am tolerably certain that

it increases in bulk and ultimately passes, in part into the first somatoblast, in part into the second. It would be interesting to investigate carefully the nature and history of this peculiar structure, but for the present I must pass it by.

2. *The Second Cleavage* (Figs. 4^a, 4, 5).

The second cleavage-plane coincides with the median plane of the adult body. It divides the smaller blastomere (*AB*) into approximately equal right and left halves (*B* and *A* respectively), and the larger (*CD*) into unequal parts. Of these, the larger (*D*), on the left side, is much larger than any of the other three; the smaller (*C*), on the right, is intermediate in size between *D* and *A* or *B*. The precise mode of formation and ultimate relation of these four cells must be accurately understood, since they determine the orientation of the embryo throughout the early development, and suggest some interesting comparisons with various other animals.

As in the case of many other eggs, the division of the smaller cell takes place slightly in advance of the other, and the respective cleavage-lines of the two cells are not precisely in the same position. The second cleavage may, in fact, best be treated, not as a single cleavage of the egg as a whole, but as consisting of two rapidly succeeding divisions of the first two blastomeres. Both divisions are of the same type as the first cleavage, the furrow first appearing on the upper side and cutting thence downwards. The smaller cell begins to divide about eighty-five minutes after the fertilization. Starting from the upper side, the furrow cuts downwards somewhat obliquely towards the left side, and finally meets the first cleavage-line to the left of the lower pole. The smaller blastomere is thus divided into two parts (*A* and *B*), of which the left (*A*) appears to be slightly the smaller when seen from above.

During the division of *AB*, the larger blastomere (*CD*) begins to divide in the same manner. At first, the furrow on the upper side is nearly or quite a continuation of the cleavage-line between *A* and *B*. As it travels downwards, however (*cf.* Figs. 4, 4^a, 5), it passes slightly to the right so as to meet the first furrow at a considerable distance to the right of the cleavage-line between *A* and *B*. Thus the first cleavage-line on the lower pole is divided into

three parts, the middle of which assumes an oblique position (*f*), and constitutes the well-known "cross-furrow" ("Brechungslinie" of Rauber), which occurs in so many eggs at this stage. Meanwhile, through a slight displacement of the four blastomeres, a cross-furrow appears on the upper pole, much shorter than the lower one and *at right angles to it.* At the completion of the division, therefore, the four blastomeres have the arrangement shown in Fig. 5.

This arrangement is of great interest with reference to the law of cleavage, and is of the utmost practical importance in the orientation. At the upper pole *B* and *D* are separated, while *A* and *C* are in contact along the short cross-furrow, *which passes from left to right.* On the lower hemisphere, this arrangement is reversed, *B* and *D* being in contact along the cross-furrow, *which passes from right to left* (viewed from the upper pole), while *A* and *C* are separated. The significance of this arrangement will be discussed in Part X, and I will here only point out its importance as a means of orientation. Owing to the fact that the four primary entomeres do not divide, the lower cross-furrow remains unaltered up to a stage when the prototroch is in full activity, the mouth, eyes, and mesoblast-bands have been formed, and the segmentation of the body has become apparent (see Pl. XX, Figs. 85, 86, and preceding figures). Thus the relations of the four-celled stage to the trochophore are, I believe, unmistakable, and all the intermediate stages may be oriented with perfect certainty by means of the position of the furrow, taken in connection with the size and arrangement of the cells. Furthermore, the slight acceleration in the division of the smaller of the first two blastomeres is a safeguard against error in determining the relations of the four-celled stage to the first two cleavage-planes. I believe, therefore, that I can state with absolute certainty that the second furrow coincides with the median plane of the larval and adult bodies.

Side views of the four-celled stage (Fig. 6) show that the difference in size between the large blastomere and the others is much greater than appears from the polar view, since its vertical diameter is greater than that of the others. The oil-drops lie far down in the blastomeres, the upper portions of which still have the same structure as in the unsegmented egg.

3. *The Third Cleavage.*

In the third cleavage, which takes place about one and three-quarters hours after fertilization, the spiral character first comes clearly into view. Each of the blastomeres divides somewhat obliquely (Fig. 7^a) into unequal parts, a smaller upper micromere, which contains none of the large oil-drops, and a larger macromere below. The four micromeres thus formed (a^1, b^1, c^1, d^1), I shall call the first group of micromeres. From them arise the entire upper hemisphere of the trochophore, the head-kidneys, and the cells of the prototroch.[1]

Side views at the moment of division (Fig. 7^a) show that each micromere is displaced somewhat towards the left. This displacement increases during the division, and reaches a maximum during the succeeding resting stage (Figs. 10, 11, 12), when the four micromeres alternate with the macromeres. [This is only approximately true, since the left posterior micromere (d^1) only slightly overlaps the anterior macromere, A.] The displacement may be described as a rotation of the four micromeres through an angle of 45° to the right [the embryo being viewed from above], and the cleavage as a whole may be characterized as a right-handed spiral — *i.e.* following the hands of a watch.

I have examined the transition from the four-celled to the eight-celled stage with especial care, in order to determine if possible whether the rotation of the micromeres (which is a very common phenomenon in other animals) is a purely mechanical process caused by pressure, etc., or is rather a result of the internal phenomena of division. The result leaves little doubt that external mechanical causes cannot be regarded as the only cause of the rotation, since *the nuclear spindles show the spiral arrangement before there is any external sign of division.* Fig. 7 (from a hardened and stained specimen) shows a four-celled stage from the upper pole, immediately before the division. The upper poles of the spindles are represented by the centres of the stars, the lower by the small circular outlines. Of the four

[1] Von Wistinghausen asserts that they give rise only to the cerebral ganglia with their appendages, and hence terms them "encephaloblasts." If this be true, the development of *N. Dumerilii* must differ to an extraordinary degree from that of the American species; but it appears to me that v. Wistinghausen gives very little evidence in support of his conclusion. (See p. 435.)

spindles only that in *C* has a radial position. The other three are oblique, and already show clearly the direction of the future divisions. Figs. 8 and 9 represent in two positions an embryo in the closing stages of the division, and show the increased obliquity of the spindles. Figs. 10, 11, 12 are the completed eight-celled stage. *The primary cause of the rotation, therefore, lies within the cells*, though it may be heightened by external causes operating at the time of division, or subsequent to it.

It is an interesting fact that the two posterior micromeres, c^1 and d^1, are usually (but I believe not always) formed slightly earlier than the others. This is the first indication of a tendency, henceforward more and more marked, towards an acceleration of development in the products of the two posterior macromeres, which may be followed up to a late stage. This fact, which has been observed in embryos of several mollusks and polyclades, is especially noteworthy in the case of *Nereis*, since the *anterior* of the two primary blastomeres is always the first to divide (again as in some mollusks and polyclades); and, moreover, it is the posterior region of the annelid that in later stages longest retains the embryonic character.

4. *The Fourth Cleavage* (Figs. 13 to 18).

The fourth cleavage, which takes place about two and one-half hours after fertilization, is of extreme importance, since of the eight new blastomeres five can be identified as definite protoblasts, each of which form a new point of departure. The essential features of the cleavage are as follows: The four micromeres divide unequally in a right-handed spiral, while the four macromeres divide unequally in a left-handed spiral. An examination of Figs. 13 to 17 will obviate the need of a detailed description. The four smaller cells derived from the micromeres ($a^{1.1}$, b,$^{1.1}$ c,$^{1.1}$ $d^{1.1}$) (blue) *are the parent-cells of the prototroch, and hence may be termed trochoblasts.*

The four new cells derived from the macromeres (a^2, b^2, c^2, d^2 or X) may be called the second group of micromeres. Three of them (a^2, b^2, c^2) are of nearly equal size; the fourth (d^2 or X, colored brown throughout the plates) is much larger, and will henceforward be termed the *first somatoblast.* The three smaller micromeres give rise to the stomodæum and to a portion of the

ectoblast of the lower hemisphere. *The large posterior micromere or first somatoblast gives rise to the entire ventral plate of the larva, and hence to its products, the ventral nerve-cord, the seta-sacs, and probably a portion of the nephridia.*

The position of these cells should be clearly understood (*cf.* Figs. 14 and 17). The lower hemisphere is occupied by the four macromeres, *A*, *B*, *C*, *D*, which have the same arrangement as in the four-celled stage, the lower cross-furrow remaining quite unchanged. The nucleus of each lies in its upper portion (Fig. 17), towards the left side, as seen in side view. Around the upper pole lie the four primary micromeres (a^1, b^1, c^1, d^1) with the four trochoblasts adjoining them. Of the three smaller micromeres of the second group (a^2, b^2, c^2), b^2 lies in the median line in front, opposite the cleavage-line between *A* and *B*, while a^2 and c^2 lie symmetrically, one on either side, a^2 opposite the cleavage-line between *A* and *D*, c^2 opposite the corresponding line between *B* and *C*. The first somatoblast, *X*, which has assumed an oval form, occupies the posterior region of the embryo, opposite the cleavage-line between *C* and *D*, but *somewhat to the left of the middle line.* This slightly asymmetrical position of *X* is not only perfectly constant in this stage, but it may be traced for a long time in the progeny of *X*. Ultimately, however, it is rectified, and the numerous descendants of *X* are bilaterally arranged with respect to the median line of the body.

It is clear, however, that *in the sixteen-celled stage the embryo is not bilaterally symmetrical.* The arrangement of the cells is radial, but in such wise that the radii do not pass straight outward from the principal axis, but are bent to one side. This arrangement, which may be termed a spiral symmetry, is retained up to a late stage.

Extremely clear optical sections are afforded by the acetic-glycerine specimens after staining with Schneider's carmine. They show (Fig. 18) that there is no trace of a segmentation-cavity, all the cells being accurately fitted together. The protoplasm, in such preparation, shows marked differentiations. That of the primary and secondary micromeres and of the trochoblasts is granular and reddish in color. In the somatoblast the granulation of the protoplasm is coarser and the color somewhat deeper, so that there is a marked contrast between it and the others. In unstained specimens this contrast is still greater,

since the protoplasm of the somatoblast assumes a brownish tint. In either case the somatoblast can always be recognized at a glance. In the macromeres the protoplasm is now differentiated into two distinct portions, separated by a very definite boundary, — an upper granular portion, in which the nucleus lies, and a lower clear portion containing the fat-drops. The boundary-line is very irregular, since the granular protoplasm sends numerous pseudopodia-like processes into the clear substance. In living specimens deutoplasm-spheres can still be seen in all of the cells, but they have diminished in number and are less conspicuous than in earlier stages.

5. *The Fifth Cleavage* (Figs. 19 to 26).

Up to this point all of the blastomeres divide nearly simultaneously at each cleavage. Henceforward the divisions are no longer synchronous throughout the embryo. The mosaic character of the development comes more and more plainly into view, and it soon becomes necessary to consider the cleavage not as a whole, but as a series of parallel cytogenies, each of which takes its origin in a group of blastomeres as in a single protoblast. A definite thirty-two-celled stage is, nevertheless, attained, and we may therefore speak of a "fifth cleavage."

The thirty-two-celled stage is attained by a series of steps which follow a definite but not invariable order. *First*, the four central micromeres (a^1, b^1, c^1, d^1) divide unequally in a left-handed spiral (Fig. 19), thus giving rise to four smaller cells ($a^{1.2}$, $b^{1.2}$, $c^{1.2}$, $d^{1.2}$) that alternate with the four trochoblasts ($a^{1.1}$, $b^{1.1}$, $c^{1.1}$, $d^{1.1}$) and form with them an eight-celled girdle that completely surrounds the central micromeres (Fig. 20). Every stage of this division may be clearly observed in preparation by means of the nuclear figures, which are very large and distinct. The spindles have from the first the spiral arrangement shown in Fig. 19, and the position of the newly formed cells is thus predetermined before the parent-cell shows any external sign of constriction.

Second, immediately following the last division (Fig. 20), or sometimes simultaneously with it (Figs. 21, 22), the somatoblast [X] buds off a small cell (x^1) at its right-hand apex, and at the same time the two posterior micromeres of the third

group (c^3, d^3) are budded forth from C and D, respectively as shown in Figs. 20, 21, 22. The embryo now consists of twenty-three cells, of which two are median (X, b^2), ten are on the left side, and eleven on the right side. A study of the position of the spindles shows that the two new micromeres are budded off in a right-handed spiral like the first set. (The nuclear stars and spindles lie, of course, in the granular portion of the macromeres.)

Third, the two anterior micromeres of the third group (a^3, b^3) are budded forth, in a right-handed spiral, from A and B respectively. At the same time the four trochoblasts divide in a meridional plane (Fig. 23), so that the girdle (colored blue) now consists of twelve cells (twenty-nine-celled stage).

Fourth, the three smaller micromeres of the second group (a^2, b^2, c^2) divide approximately in a meridional plane (somewhat oblique), thus completing the thirty-two-celled stage (Figs. 24, 25, 26; the last two, however, are already in transition to the thirty-six-celled stage).

A careful study of the embryo through these changes shows that all of the cell-divisions conform to the spiral type. This is at once apparent in the divisions of the four macromeres and of the four primary micromeres. It is also easily seen in the divisions of the secondary micromeres (a^2, b^2, c^2, X). Each of them divides somewhat obliquely (*cf.* Figs. 25, 26, 33), so that one of the cells lies somewhat lower than the other, and in most cases the lower cell is obviously smaller than the upper. The difference in size is very great in the case of X and x^1, but is much less in the case of the others ($a^{2.1}$, $a^{2.2}$, Fig. 33). [In the specimen shown in Figs. 25, 26, on the other hand, there is no appreciable difference in size, but I have never seen a case in which the upper cell is the smaller.] If this group of cells be followed around the embryo from right to left (against the hands of a watch), the upper (larger) cell always comes first; *i.e.* the first division of the second group of micromeres takes place in a left-handed spiral, *like the second division of the first set of micromeres*.

The division of the trochoblasts, as far as I can determine, is meridional and equal; *i.e.* of a true radial type, of which the spiral type is a modification.

6. *Third Spiral Division of the Primary Micromeres; Formation of the Apical Rosette; Origin of the Second Somatoblast; Second Division of the First Somatoblast.*

The strictly spiral period of the cleavage is brought to a close by three events.

(1) The four primary micromeres (a^1, b^1, c^1, d^1) bud forth four small cells at their inner angles (at the upper pole), which arrange themselves in a very regular apical rosette, the cells of which alternate with the central micromeres (Figs. 27, 28, etc.). The position of the spindles is the same as in the first division of a^1, b^1, c^1, d^1; *i.e.* the division follows a right-handed spiral, but the character of the division is very different, since the smaller cells are formed at the central instead of the peripheral angles of the cells (*i.e.* towards instead of away from the vertical axis of the embryo). In this case the spiral character is accentuated by the fact that the cells divide in the following regular order: c^1, d^1, a^1, b^1. I have observed this several times in the living embryo, and I have also obtained several preparations like Fig. 27, in which the order of division is completely shown by the nuclear figures. (*Cf.* also Figs. 25, 26.) At a later period the apical tuft of cilia appears exactly at the point where the rosette is formed, and there can be no doubt that it arises, in part at least, from the rosette-cells. I have not been able, however, to trace the connection in detail. An almost exactly similar rosette is formed in the polyclade *Eurylepta* (Selenka, No. 22), but its fate is doubtful.

(2) During the formation of the rosette (or sometimes somewhat later) the somatoblast buds forth at its *left* apex a small cell (x^2) which lies symmetrically with x^1 (Figs. 25, 29, 31).

(3) After a short pause, a large granular cell (*M*, Figs. 29, 31, 33, 34), somewhat smaller than *X*, is budded off obliquely from the left posterior macromere (*D*). *This cell is the second somatoblast or primary mesoblast, from which the mesoblast-bands are formed.* It lies below *X* (*i.e.* anterior to it), and considerably to the left of the median line (*i.e.* the cleavage-line between *C* and *D*). Its exact position and mode of formation may be seen by a comparison of Figs. 29, 31, 33, 47, and 48.

The formation of the second somatoblast ends the spiral period of development, and it is a very significant fact that the

close of this period marks also the complete differentiation, not only of the germ-layers, but also of many of the protoblasts from which the adult organs arise. The segregation of the embryonic material is in fact so nearly completed, that this last spiral stage may be taken as a new point of departure. The embryo (Fig. 29) now consists of thirty-eight blastomeres, as follows (*cf.* also the diagram, p. 440):

4.	The macromeres *A*, *B*, *C*, *D*, or entomeres	= Entoblast.
4.	The first group of micromeres, a^1, b^1, c^1, d^1,	Ectomeres = Ectoblast.
8.	The products of the trochoblasts, $a^{1\cdot1\cdot1}$, $a^{1\cdot1\cdot2}$, $b^{1\cdot1\cdot1}$, $b^{1\cdot1\cdot2}$, $c^{1\cdot1\cdot1}$, $c^{1\cdot1\cdot2}$, $d^{1\cdot1\cdot1}$, $d^{1\cdot1\cdot2}$,	
4.	The four intermediate girdle-cells, $a^{1\cdot2}$, $b^{1\cdot2}$, $c^{1\cdot2}$, $d^{1\cdot2}$,	
4.	The rosette-cells, $a^{1\cdot3}$, $b^{1\cdot3}$, $c^{1\cdot3}$, $d^{1\cdot3}$,	
3.	The three smaller secondary micromeres, $a^{2\cdot1}$, $b^{2\cdot1}$, c^{21},	
3.	The stomatoblasts, $a^{2\cdot2}$, $b^{2\cdot2}$, $c^{2\cdot2}$,	
3.	The first somatoblast (X) and its progeny (x^1, x^2),	
4.	The four tertiary micromeres (a^3, b^3, c^3, d^3),	
1.	The second somatoblast or mesomere	= Mesoblast.

38

Each of these ten categories of blastomeres might be taken as the starting-point for a separate description. Practically, however, it will be useful to pursue the general development somewhat further before turning to the history of the individual cytogenies. The embryo may now be termed a "gastrula," in so far as it consists of an "inner" and an "outer" layer. If I employ this term, it is, however, solely for the sake of convenience. The embryo is "two-layered" only in a conventional sense. The "outer layer" is a mes-ectoblast in which the two constituents are completely separate. The origin of the mesoblast in *Nereis* is ectoblastic (because it forms a part of the "outer layer"), or entoblastic (because it arises from one of the four entomeres), or neither (because it forms the lip of the "blastopore"), according to the reader's preference.

IV. Transition to the Bilateral Period.

As far as the development of the permanent organs is concerned, the transition from the spiral to the bilateral type of development is remarkably abrupt. It is only in the peculiar changes involved in the formation of a larval organ, the prototroch, that the spiral form of division overlaps the bilateral

period and necessitates the recognition of an intermediate stage. The formation of the prototroch is, however, so intimately connected with the first bilateral cleavages of the upper hemisphere that they must be described together.

1. (*a*) *Bilateral Division of* c^1 *and* d^1; (*b*) *Third division of the First Somatoblast;* (*c*) *Fission of the Second Somatoblast* (Figs. 30–32).

These three events occur nearly at the same time (about six hours after fertilization), though there is a certain amount of variation. (*a*) The first bilateral division always takes place in the two posterior primary micromeres (c^1 and d^1), which divide transversely into unequal parts, the anterior being the smaller. The spindles are exactly radial in position (*cf.* the spindles in the same cells in the last spiral cleavage, Fig. 27), and the anterior cells ($c^{1.4}$, $d^{1.4}$, Figs. 31, 32, 35) are perfectly symmetrical with respect to the second cleavage-plane, which now forms the median plane of the body. Since the posterior cells (c^1, d^1) long retain their superiority in size, we may continue to call them the posterior primary micromeres. The four cells thus produced form, as it were, an arch (Diagram II, p. 396), the ends of which rest upon the girdle-cells, while the keystone is formed by the posterior rosette-cell ($d^{1.3}$).

(*b*) Meanwhile a curious event happens, the exact nature of which I only made out after repeated examination, both of living specimens and of preparations. The first somatoblast (X), namely, buds forth a small cell (x^3) from its posterior or dorsal border in the median line. *This cell pushes before it the posterior intermediate girdle-cell* ($d^{1.2}$), *which is thus carried up into the arch formed by* d^1, $d^{1.4}$, $d^{1.3}$, $c^{1.4}$, c^1, *and loses its connection with the girdle* (Fig. 31). The girdle is thus reduced from twelve to eleven cells, and is interrupted in the median posterior (dorsal) line. We shall see hereafter that this interesting occurrence *is the cause of the median interruption of the prototroch* that appears to be a common feature of the trochophore larva. As a rule, this division of X takes place simultaneously with the bilateral division of c^1, d^1, and the sudden transformation of the postero-dorsal region is, in the living embryo, an interesting spectacle. Sometimes, however, the division of X follows the others, as in Fig. 31.

(*c*) In the third place, soon after the events just described, the second somatoblast or mesomere divides into equal parts (*M.M.*, Figs. 32, 48, 49, 50). These are the primary mesoblasts, which give rise to the mesoblast-bands.

The embryo now consists of forty-two cells. Though a distinctly bilateral arrangement is now apparent, the peculiar displacement of the somatoblasts towards the left is still apparent, and it is only gradually overcome as the development progresses.

2. *History of the First Group of Micromeres. Origin of the Cross and of the Prototroch.*

It will be useful at this point to recapitulate the history of the girdle, since it is immediately connected with the origin of the prototroch. The four primary micromeres first give rise (at the fourth cleavage) to four smaller cells, the trochoblasts ($a^{1.1}$, $b^{1.1}$, $c^{1.1}$, $d^{1.1}$) in a right-handed spiral division (Figs. 13, 14), and, then (at the fifth cleavage), in a left-handed spiral division, to four similar cells alternating with the trochoblasts, which may be called the intermediate girdle-cells ($a^{1.2}$, $b^{1.2}$, $c^{1.2}$, $d^{1.2}$). Thus a girdle of eight cells is formed that surrounds the central micromeres (Fig. 20). [In the figures the trochoblasts are colored a deeper blue than the others.] Later, in the course of the fifth cleavage, the trochoblasts divide in a meridional plane (Fig. 23), so that the number of cells in the girdle increases from eight to twelve.

When fully formed the prototroch is likewise found to consist of twelve cells, and I at first supposed that they were identical with the twelve girdle-cells. Further investigation proved, however, that *the four intermediate girdle-cells are drawn out of the girdle, and the prototrochal cells are formed from the eight remaining cells, derived from the trochoblasts.*

In the eight-celled girdle (Fig. 20) the cells are very regularly arranged, two girdle-cells lying opposite each micromere. After the division of the trochoblasts, however, the intermediate girdle-cells are gradually displaced, so that they first come to lie opposite the intervals between the micromeres, and then begin to extend up between them (*cf.* Figs. 23 to 30, and Diagram II). The posterior median girdle-cell is the first to be drawn out of the girdle, being pushed up between the products

of c^1 and d^1 by the median division of X, as already described (Figs. 31, 32).

Shortly after the bilateral division of the posterior micromeres, c^1 and d^1, a similar bilateral unequal division takes place in the anterior pair a^1 and b^1 (Figs. 35 to 38, Diagram II). As this takes place, the micromeres move apart both from each other and from the posterior micromeres so as to form an extremely regular and symmetrical cross, the centre of which is occupied by the apical rosette. The three remaining intermediate girdle-cells ($a^{1.2}$, $b^{1.2}$, $c^{1.2}$) are at the same time drawn up into the angles between the arms of the cross, and thus recede from the girdle, though they do not leave it entirely until somewhat later. This will be rendered clear by the accompanying diagram (No. II).

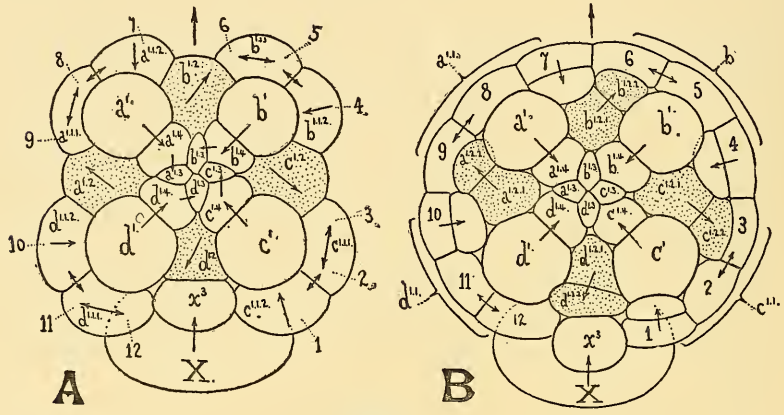


Diagram II.

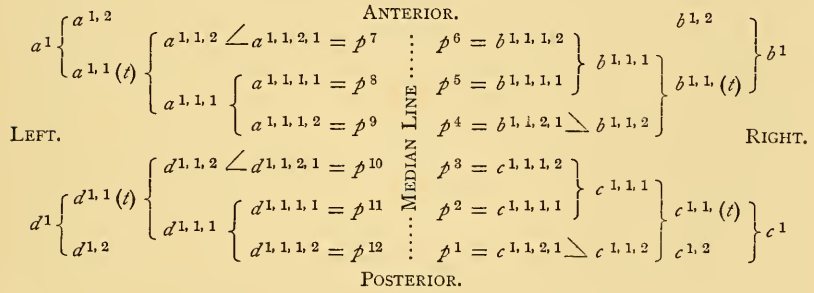
The shaded cells represent the intermediate girdle-cells and their progeny.

Nearly at the same time, the entire set of girdle-cells divide in a very interesting symmetrical manner, which is illustrated by the diagram and is shown in Figs. 35, 36, 39. In Diagram II, *A* (*cf.* Fig. 35) the direction of the division-spindles is shown by the arrows. Diagram II, *B* (*cf.* Fig. 39), shows the result. It will be seen that each intermediate girdle-cell divides in a somewhat oblique plane, and is at the same time completely drawn out of the girdle. The products of the trochoblasts meanwhile divide in such wise that in each pair of cells one divides horizontally and one vertically, in regular succession in a left-handed spiral around the girdle. Thus each of the origi-

nal trochoblasts gives rise to four cells, of which three remain in the prototroch, and the fourth lies above it in the upper hemisphere of the larva. The twelve prototrochal cells thus fall into four groups of three each, which are at first distinctly separated from each other (*cf.* Figs. 38, 41). The gaps soon close up, however, *excepting the posterior, which persists as the well-known interruption in the median dorsal (posterior) line.*

The examination of a large number of embryos has led me to believe that this law of division is perfectly constant. The order of division varies considerably, as is shown in the figures. Thus in Fig. 32 some of the posterior girdle-cells have already divided, while the anterior micromeres and girdle-cells are still quiescent, and only occasionally is a specimen found that shows the divisions as completely as in Figs. 35, 36. The division-planes, however, appear to vary only within very narrow limits.

The following scheme shows the derivation of the prototrochal cells and brings out certain curious points in their mode of origin (see also the general cytogenetic tree, p. 382).



An inspection of this scheme brings out the fact that although the prototrochal cells are bilaterally symmetrical in position, they are not so in origin, since the brackets on the two sides do not correspond. The unlettered lines lead to the cells expelled from the prototroch in the horizontal divisions (*cf.* Figs. 27, 35, 39).

The significance of the prototroch-formation remains to be seen, since nothing is known of the phenomena in other forms. The number of prototrochal cells has not hitherto been determined with certainty in a single form. Hatschek (No. 10), confirmed by Fraipont (No. 8), describes the prototroch of *Polygordius* as consisting of numerous cells. Von Drasche (No. 5)

gives several figures of the larva of *Pomatoceros*, in which the numbers of the prototrochal cells are respectively 19, 18, 17, and 15, but he does not appear to have given special attention to the point. In *Eupomatus* Hatschek figures specimens with 10, 9, and 8 prototrochal cells, but makes no mention of their number in the text. Kleinenberg states that in *Lopadorhynchus* there are usually fourteen nuclei in the prototroch (the cell-outlines could not be distinguished). The only form that I have carefully examined, besides *Polygordius* and *Nereis*, is *Hydroides* (*Serpula*) *dianthus*, Verrill, in which the prototrochal cells of the young free-swimming trochophore are eight in number.

It is easy to suggest comparisons between the eight-celled prototroch of *Hydroides*, the eight-celled girdle of *Nereis*, the eight series of vibratile plates in the Ctenophore, etc., but such comparisons have no value on account of the paucity of data. It would, however, be very interesting to investigate the comparative development of the prototroch, for it is certain that the cells vary in number in different annelids. If Kleinenberg has correctly determined their number in *Lopadorhynchus*, it would seem that they must arise by a different law of cell-division from that of *Nereis*, since the number of cells is not a multiple either of three or of four.

It will be convenient to proceed directly to a brief sketch of the later history of the prototroch. The original girdle lies considerably above the equator of the embryo, but the prototrochal girdle gradually passes downwards until it takes a nearly equatorial position. The cells become somewhat elongated and numerous vacuoles appear in them. About the tenth or eleventh hour the cilia appear and the larva begins to rotate slowly (Fig. 60). As in the case of many other annelids, the cilia are put forth through pores in the egg-membrane, which appears to persist as the cuticle of the adult worm. The development of the cilia is very sudden, the operation requiring only a few minutes. At the same time the apical cilia are put forth in the following curious manner. The egg-membrane is at this period separated from the upper side of the embryo by a considerable space. A narrow process is now rather suddenly put forth from the middle of the upper hemisphere (Fig. 60). This process is extended until it comes into contact with the mem-

brane, over a small area from which the cilia are immediately put forth. At this stage the embryo recalls the larva of *Sipunculus* at the time of the amnion-formation (see Hatschek, No. 11). The space surrounding the apical tuft is, however, soon obliterated, and the larva again becomes spherical and closely surrounded by the membrane. It seems possible, nevertheless, that this peculiar process may give the key to an explanation of the origin of the amnion in other forms.

The prototrochal cilia are put forth from the large cells alone and not from the adjoining smaller cells. Nevertheless, the girdle of large cells is accompanied by a second girdle of smaller cells lying just above it. It is only in later stages that this auxiliary row becomes clearly defined (see Figs. 77, 78, 82), when the cells are found to correspond accurately in number and position with the large cells. I much regret my failure to determine their origin, and this is one of the greatest gaps in my work. Their precise correspondence in position with the large cells makes it seem probable that they are derived from the latter by horizontal divisions; but, except in the case of $a^{1.1.2}$, $b^{1.1.2}$, $c^{1.1.2}$, and $d^{1.1.2}$, I have never seen the least evidence of such a division, although a large number of embryos were examined to determine the point. This may perhaps be taken as indirect evidence that the auxiliary cells are differentiated from the cells of the upper hemisphere — *i.e.* from the products of the intermediate girdle-cells and from the four arising by the horizontal divisions of $a^{1.1.2}$, etc. This conclusion is, however, of too great importance to be accepted on purely negative evidence and must be tested by future research. The origin of the ring-nerve and of the ring-muscle I have not yet studied.

V. Bilateral Period of Cleavage.

With the completion of the prototroch, the cleavage loses every trace of the spiral symmetry of earlier stages, and becomes strictly bilateral. The median plane, with respect to which the bilaterality manifests itself, is the plane of the second cleavage, which finally persists as the median plane of the adult body. Hence the appearance of the bilateral divisions is the first definite step in the long series of changes by which the spirally symmetrical embryo is converted into the bilateral adult.

Nevertheless, although the *form of cell-division* is strictly spiral up to the thirty-eight-celled stage, an adult bilaterality is foreshadowed, long before the bilateral divisions begin, in the arrangement of the cells. The anterior macromeres are symmetrically placed with reference to the future median plane, and so in a certain sense are the primary micromeres, though this is somewhat obscured by their rotation to the right. I may call especial attention, however, to the fact that they gradually move back into their original position (*cf.* Figs. 20, 23, 28), and are thus symmetrically placed, with reference to the median plane, before the close of the spiral period. This proves that *the rotation is but a temporary effect of mechanical conditions, and hence has no morphological meaning.*

Up to the close of the spiral period, however, the embryological material is not equally distributed on either side the future median line, mainly on account of the storage of the substance of the somatoblasts in the left posterior macromere. *Upon the separation and transference of this substance to the middle line, the asymmetry disappears, the posterior pair of entomeres being equal, like the anterior pair* (*cf.* Figs. 47, 48, 51, 55–57, 86). *Immediately afterwards the bilateral divisions begin.* This I believe to be one of the most significant and important points in the entire ontogeny.

1. *General History of the Upper Hemisphere. Origin of the Head-Kidney.*

The *first bilateral division* of the four primary micromeres and the origin of the cross have been described at p. 395. Attention may be again called to the fact that the division of the posterior micromeres (c^1, d^1) takes place some time before that of the anterior pair (a^1, b^1). *The second bilateral division of c^1 and d^1 gives rise to a pair of cells, from which arise the head-kidneys;* I shall therefore term them the *cephalic nephroblasts.* These cells (Figs. 37, 38, $c^{1.5}$, $d^{1.5}$, colored orange) are smaller than c^1 and d^1, and from the first differ from them in structure, the protoplasm being clear and watery, and showing a marked tendency to vacuolation. Shortly after this division of c^1, d^1, the anterior pair of micromeres (a^1, b^1) divide in a similar manner (Figs. 39, 40), giving rise to $a^{1.5}$ and $b^{1.5}$ respectively. At this time the

upper hemisphere contains a beautiful and symmetrical cross of cells, the four arms of which, inclined at an angle of 45° to the median plane, are the products of the four primary micromeres, a^1, b^1, c^1, d^1 respectively. The centre of the cross is occupied by the apical rosette, and each arm consists of three cells, the terminal of which is larger than the others, like a teloblast, and may still be regarded as the parent micromere. For the sake of brevity, I shall henceforward call them the *pole-cells* of the cross. The middle cell of each posterior arm is the *nephroblast* (henceforward designated as *n*).

The pole-cells still lie in contact with the prototroch ; the interspaces between the arms of the cross and the prototroch are occupied by the descendants of the intermediate girdle-cells, which I have not succeeded in following in detail beyond the stage shown in Fig. 41.

The later history of the cross may be briefly treated. Both the pole-cells and their derivation continue to divide bilaterally as long as the individual cells can be followed ; but, owing to the appearance of longitudinal divisions (*i.e.* parallel to the arms of the cross) in the cross-cells (*cf.* Figs. 40, 41), and to divisions in the descendants of the intermediate girdle-cells, the outlines of the cross become less distinct and finally quite indistinguishable. The pole-cells likewise ultimately disappear ; the anterior pair are lost first, while the posterior pair persist, and continue their symmetrical divisions up to a late period (Fig. 59).

The second bilateral division of a^1, b^1 is accompanied by an oblique division of $c^{1.4}$, $d^{1.4}$ (Fig. 39). This is followed by *the third bilateral division* of c^1, d^1 (giving rise to $c^{1.6}$, $d^{1.6}$, Fig. 40), which is nearly longitudinal (with respect to the arms of the cross). At the same time, $a^{1.4}$ and $b^{1.4}$ divide longitudinally (Fig. 40). Next, $a^{1.5}$ and $b^{1.5}$ divide in the same plane (Fig. 41), and a little later the anterior pole-cells divide (Fig. 41) in an approximately transverse plane.

At this stage each of the original primary micromeres has undergone three spiral and three bilateral cleavages, in the last four of which the posterior pair (c^1, d^1) invariably preceded the anterior pair. Beyond this point I have not been able to follow the anterior pair (a^1, b^1), since they become lost amongst the surrounding cells. *The fourth bilateral cleavage* of c^1, d^1 (giving rise to $c^{1.7}$, $d^{1.7}$, Figs. 42, 43, 44) is nearly at right angles to

the last, as shown in the figures. Later bilateral divisions of c^1, d^1 are shown in Figs. 45 and 59, but I have not followed them in detail beyond the seventh division. There can be no doubt that the cross gives rise in large part to the cerebral ganglion. For a further account of it see p. 421.

The descendants of the intermediate girdle-cells have meanwhile continued to divide so as to fill the interspaces of the cross, but I have thus far not attempted to follow this history in detail.

2. *History of the Head-Kidney.*

We may now return to the history of the cephalic nephroblasts ($c^{1.5}$, $d^{1.5}$). From their first formation these cells are overlapped by the adjoining cells, and as the development proceeds they soon sink below the surface, and are finally entirely covered in (Figs. 38 to 45). The protoplasm meanwhile becomes clear and vacuolated and shows so marked a contrast to that of the adjoining cells that after a little practice the nephroblasts may, in good preparations, be distinguished at the first glance. In the Schneider-acetic preparations every stage of the enclosure may be clearly followed, especially in the side-views, where the exact relation of the nephroblast to the adjoining cells may be seen in optical sections by rolling the embryo from side to side. The nephroblasts meanwhile become more elongated and somewhat pointed at the ends. After sinking below the surface they slowly migrate outwards and downwards towards the prototroch, forcing their way between the outer layer of cells and the four entomeres. In this way they pass downwards until they lie quite in the lower hemisphere below the prototroch (Figs. 74–76), where the remainder of their development is accomplished.

After taking up its position below the prototroch (Fig. 75) the nephroblast rapidly elongates, extending itself forwards and backwards between the outer cells and the entomeres. It is thus converted into an elongated organ which extends about half-way around the body (Figs. 62, 63, 75–77, 79, 80–84).

Mention has already been made of the vacuolation of the protoplasm of the nephroblasts. As far as I have observed, the vacuoles always appear at one side of the cell (Figs. 74, 75), the nucleus being crowded to one side. As the nephroblast

elongates (Fig. 76), the vacuoles coalesce so as to form a sinuous canal in the protoplasm. As the elongation proceeds, the canal becomes narrower and more distinct, and the head-kidney is thus converted into a slender tube (Figs. 77, 81, 82). Up to the stage shown in Fig. 76 the head-kidney is certainly unicellular; whether the nucleus divides in later stages I cannot say.

When fully formed, the head-kidneys entirely surround the body and again lie partly inside the prototroch, as in Fig. 82. Near their anterior ends (which appear always to overlap, as shown in Fig. 79), they expand somewhat and then taper to a blunt point. Their posterior ends (Figs. 67 to 70) are pointed and terminate near the gap in the prototroch. In the latest stages in which I have observed it (Fig. 89) the head-kidney lies completely inside the prototroch, considerably flattened against the cells of the latter. Its ultimate fate remains undetermined.[1]

[1] I have termed this organ the head-kidney only with a certain reservation, since I have not succeeded in observing any evidence of cilia in the cavity, or any sign of an external opening. It is, however, very difficult to explore the interior of the organ in the living embryo on account of the confusion produced by the active vibrations of the prototrochal cilia; and the external opening of the head-kidney in other forms is notoriously difficult to see. The only other structures with which it might be confounded are the ring-nerve and the ring-muscle, with the appearance of which in other annelid trochophores I am familiar. Neither the effect of methyl-blue nor of osmic acid gives decisive results. The protoplasm shows no longitudinal striation, and the canal always distinctly appears.

It should be added that I have not been able to see either ring-nerve or ring-muscle in the *Nereis* trochophore. That the muscle is really absent is indicated by the fact that the prototrochal region is never contracted either in preserved specimens or in living larvæ, however the latter may be stimulated.

In view of the peculiar mode of origin of the "head-kidneys," I may be permitted a few words of explanation. I had observed various stages of the enclosure and migration of the nephroblasts in scores of specimens before realizing the true nature of the process, for such a migration seems from an *a priori* point of view so improbable that the possibility never occurred to me, especially as I had looked for a wholly different origin for the head-kidney. In the earlier stages I had often observed the nephroblasts projecting below the ectoblast, and in later stages the developing head-kidneys lying below the prototroch. The disappearance of the nephroblasts from their original position I supposed to be caused simply by their withdrawal into the ectoblast. I was led to the discovery of what actually occurs first, by my failure to account for the nephroblasts in the surface-views, and second, by finding stages like Fig. 74, where the nephroblast lies directly inside of the prototroch. A careful examination of the preceding stages soon showed every transition, and I believe that whatever doubt may exist as to the nature of these organs, there can be none as to their mode of origin.

Before leaving the head-kidney I may add that the vacuolation and granulation of the prototrochal cells suggest that they, too, may possess an excretory function, as has been pointed out by Hatschek in the case of *Polygordius* (No. 10). The marked tendency to vacuolation in the post-trochal cells (unfortunately I am not able to state whether the vacuoles exist in the living embryo) suggests a comparison with the so-called external or post-velar excretory cells of the molluscan veliger, with which they agree in position. In the Mollusca the cells of the velum itself are often extensively vacuolated, and it has been suggested (for a review of the literature see *McMurrich*, No. 17) that the velar cells, the post-velar cells, and the head-kidneys originally formed part of one system concerned especially with the excretion of waste matters produced by the intense activity of the velar cilia. In the Mollusca the post-velar excretory cells and the head-kidney replace one another (*i.e.* do not occur together). In *Nereis*, if the comparison has any value, the three coexist side by side, and possibly represent the primitive condition of the trochophore larva.

VI. History of the Somatoblasts. Origin of the Ventral Plate and of the Mesoblast-bands. Closure of the Blastopore. Development of the Stomodæum. (Plates XVII and XVIII.)

We turn now to the history of the lower hemisphere, in the course of which the most complicated and interesting events of the ontogeny take place. These events are so intimately bound together that it will be necessary to give first a brief *resumé*.

The boundary between the upper and lower hemispheres is formed by the prototroch which, as has been shown, is a product of the first group of micromeres. The superficial cells of the lower hemisphere are therefore wholly derived from the second and third sets of micromeres and from the products of the second somatoblast.

After the formation of the second somatoblast (*i.e.* at the end of the spiral period, Figs. 29, 31, 33, 49) there are in all fourteen of these cells, viz. :—

The three smaller secondary micromeres and their progeny ($a^{2.1}$, $a^{2.2}$, $b^{2.1}$, $b^{2.2}$, $c^{2.1}$, $c^{2.2}$).

The first somatoblast (X) and its progeny (x^1, x^2).

The third group of micromeres (a^3, b^3, c^3, d^3).

The second somatoblast (M).

The arrangement of these cells with respect to the blastopore is shown in Diagram III. The entomeres are considerably more than half enclosed by the other cells (Figs. 33, 34), and the open space may be called the blastopore. It will be seen from the diagram and from a comparison of the figures, that the blastopore is somewhat asymmetrical, and that its hinder lip (which is formed by the second proteloblast) lies somewhat posterior to the lower pole (which lies in the middle of the cross-furrow).

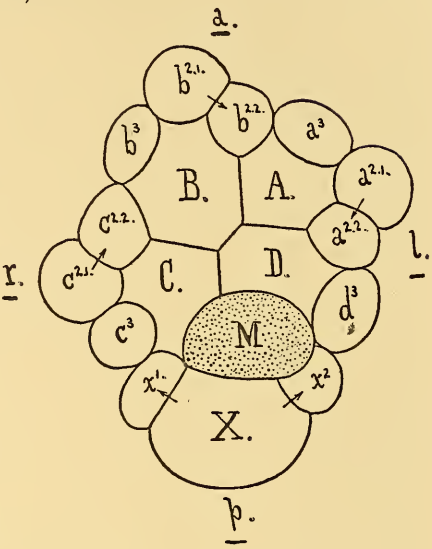


DIAGRAM III.

The closure of the blastopore takes place precisely at the lower pole (Figs. 55–57) *by convergence of the cells from all sides*, though the shape and position of the blastopore are such that the principal growth of the cells during the closure takes place from in front backwards (*i.e.* as in *Rhynchelmis* or *Clepsine*, and not as in *Lumbricus*).

The margin of the blastopore is formed at first by all of the cells of the lower hemisphere excepting x^2 (*cf.* Diagram III and Figs. 25, 26, 31, 33). As it narrows (Fig. 56), its anterior and lateral margins are formed in part by the descendants of a^3, b^3, c^3, and d^3, and in part by three large cells (*st*) *which give rise in large part at any rate to the stomodæum, and may, therefore, be called stomatoblasts.* The stomatoblasts, for reasons to be hereafter set forth, I believe to be the cells $a^{2.2}$, $b^{2.2}$, and $c^{2.2}$, or their derivatives.

The posterior lip is formed by a group of small cells that are budded forth from the primary mesoblasts derived by the bilateral division of the first somatoblast (Figs. 56, 57). *These cells*

afterwards become pigmented (*see figures of later stages*) *and are finally pushed into the interior to form a part of the mesoblast, the remaining portion being formed from the residue of the primary mesoblasts. The mesoblast, therefore, arises from the posterior lip of the blastopore.*

Meanwhile the first somatoblast undergoes an extraordinary series of the divisions, quite constant in form and order, which give rise to the cells of the ventral plate. *The cells thus formed grow forward and cover in the primary mesoblasts, coming into juxtaposition with the small cells* (*budded from the primary mesoblast*) *that form the posterior lip of the blastopore, and that afterwards give rise to the pigment-area.*

Thus the ventral region consists of two distinct portions, viz. (1) an anterior portion derived from the primary mesoblasts, and (2) a much larger posterior portion, the ventral plate proper, derived from the products of the first somatoblast. After the mesoblasts have budded several times at the surface and are entirely covered in, the character of their division changes, each divides into two somewhat unequal parts (Figs. 61, 63), of which the lower (mesial) is somewhat the larger. By continued divisions (Figs. 79–82) the two cells on each side give rise to the two mesoblast-bands, which are continuous below with the superficial cells of the pigment-area (Fig. 70). *Ultimately the pigment-cells themselves migrate inwards, and give rise, in part at least, to the splanchnic mesoblast* (Figs. 89–91). *The longitudinal muscles arise from the mesoblast-bands;* i.e. *from the products of the primary mesoblasts after the superficial cells* (*pigment-cells*) *have been budded forth.*[1]

[1] This account of the mesoblast differs somewhat from that contained in my preliminary paper, since I at first failed to observe the superficial budding of the primary mesoblasts, and described the latter as only sinking below the surface after their first division into two. This error of detail does not, however, affect the general significance of the phenomena. I may add, at this point, that the essential point of difference between v. Wistinghausen's account and my own is that he believes some of the small cells budded forth from the primary mesoblasts to be true ectoblast-cells which remain at the surface, whereas I believe that all migrate inwards, and are, therefore, mesoblast *sensu stricto*. It appears to me that v. Wistinghausen has been unduly influenced by Kleinenberg's views on this point, and I believe that *N. Dumerilii* is a far less favorable object for the investigation of the question, on account of the lack of the pigment. My own studies are, however, not yet concluded, and I hope to study other forms before publishing further accounts of the facts in *Nereis*.

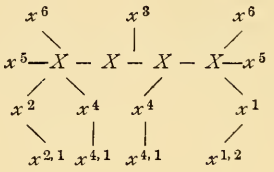
1. *The First Somatoblast.*

Nothing in the development of *Nereis* has excited my interest in a higher degree than the history of the first somatoblast, which undergoes a long series of divisions, continually changing in their character, comparable in regularity and precision with the cleavage of the ovum itself. I have followed these changes many times, both in the living embryo and in preserved specimens, and am convinced that the order and form of the divisions are almost absolutely constant. Their character is such, moreover, as to bring to the foreground some of the most interesting problems in the mechanics of cell-division.

The first three divisions have already been described, but may briefly be reviewed. The somatoblast *first* buds off a small cell (x^1) at the right side (Fig. 20), *second*, a similar cell (x^2) at the left side (Fig. 29), and *third*, a third cell (x^3) in the median postero-dorsal line (Fig. 31). These three cells are approximately 120° apart, and are nearly, but not quite, symmetrical with respect to the median line (*cf.* Figs. 32 and 48). The *fourth* division cuts the somatoblast into equal parts (Figs. 37, 38, Pl. XVI; 50, 51, Pl. XVII), which are nearly symmetrical with respect to the median plane, but always show a slight displacement towards the left. These two cells I shall call the *posterior proteloblasts* (*XX*). At the *fifth* division (Figs. 52–54) each of the proteloblasts buds forth a smaller cell (x^4, x^4) at its anterior extremity. At the *sixth* division (Figs. 42, 43, Pl. XVI) each buds forth a small cell (x^5, x^5) at its outer margin. At the *seventh* division (Fig. 54) two small cells (x^6, x^6) are budded forth at the latero-posterior angles.[1] At the *eighth* division (Figs. 46, 56–58) each proteloblast divides longitudinally into two equal parts (*XXXX*). The four cells thus formed I shall call the *posterior teloblasts*. Meanwhile x^1, x^2, x^3, and x^4, x^4 divide transversely, the result being shown in Fig. 46, Pl. XVI. The order of division varies somewhat. As a rule, x^2 (Figs. 50, 52) divides first (not x^1, as

[1] In regard to this division, there is unfortunately some uncertainty, owing to the fact, as I believe, that I overlooked the sixth division in the living embryos, and only subsequently observed it in the prepared specimens. That such a division takes place at this period in many specimens, there is no doubt. It is possible, however, that this is only a variation of the fifth division, though, in view of the precision that in general characterizes the behavior of the proteloblasts, I must regard this possibility as rather remote.

we might have expected); but sometimes the reverse is the case (Fig. 53). These are followed by x^4, x^4 (Fig. 56). At this period, therefore, the progeny of the somatoblast are approximately seventeen in number, as shown in the accompanying diagram. I say approximately, because in some cases, at any rate,



the progeny of x^2 and x^1 begin to divide before the equal division of the two X's (see Fig. 55), and it now becomes extremely difficult to distinguish certainly between them and the cells at the side of the embryo derived from the second and third sets of micromeres (*i.e.* c^3, d^3, $a^{2.2}$, $c^{2.1}$). A comparison of the figures (43, 46, 54, 55, etc.) will show the anterior x-cells passing forwards and growing over the primary mesoblasts. This is shown with perfect clearness from the side in optical section (Figs. 71 to 73, Pl. XIX). Actual sections through these stages confirm the optical sections in every respect.

During these stages the primary mesoblasts have budded several times, giving rise to the group of small secondary mesoblast-cells (Figs. 55 to 57) that form the posterior lip of the blastopore. They may be distinguished from the x-cells by their nuclei, which are smaller and appear coarsely granular on account of the character of the chromatic network. (In the figures, these nuclei are made granular, while the others are left clear.)

The *ninth* division is shown in Fig. 59. Each of the teloblasts divides transversely into unequal parts, of which the smaller is anterior. The inequality in size is much less marked than in the preceding unequal division, but it is always distinctly recognizable. This stage is usually attained from the tenth to the eleventh hour, but the specimen figured is thirteen hours old. Soon afterwards (Fig. 60) the cilia are put forth in the manner already described, and the embryo begins to rotate.

Up to this point I have repeatedly observed every division of the X-cells in the living embryos (with the exception of the

sixth, as already explained). The movements of the embryo now render this impossible, and hence the later changes have been studied mainly from preparations, though most of the stages have also been observed in the living state. At the *tenth* division (the result of which is shown in Fig. 61) each of the teloblasts again divides transversely into two unequal parts, the smaller, as before, lying in front. I do not feel certain, however, that this division really takes place (*i.e.* I may have confounded it with the last), as the cells of the ventral plate are now so numerous that it is impossible to trace the exact genetic relationships among them. The occurrence of such a division is an inference from the fact that the teloblasts are found dividing in this manner a considerable time (*i.e.* from one to two hours) after the stage shown in Fig. 59, and the cells of the ventral plate are more numerous than before. The point (which is mainly of importance in a theoretical consideration of the history of the nuclear figures) could easily be determined by a re-examination of these stages.

The *eleventh* division (the result shown in Figs. 63, 64) is one of great importance, because by it the outer pair of teloblasts disappears. Each divides lengthwise into nearly equal parts, which can scarcely be distinguished from the remaining cells of the ventral plate. I have never succeeded in finding a specimen to show the spindles of this division, and hence only infer its occurrence from the position of the cells, but I have no doubt of its occurrence. The two remaining teloblasts will henceforward be called the *residual teloblasts*.

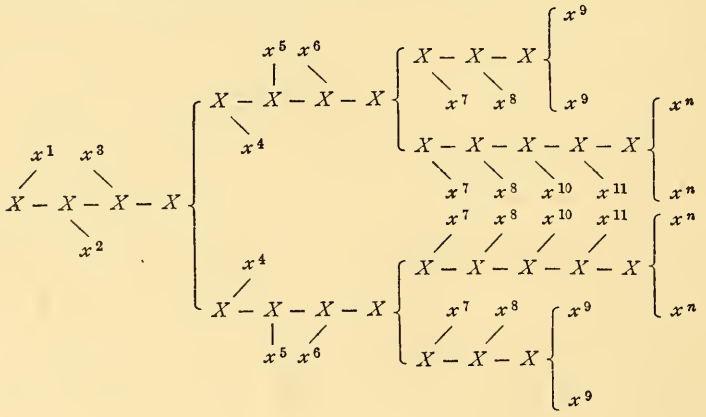
The *twelfth* division (Figs. 65, 66) marks another important step; viz. the *divergence of the residual teloblasts*. Each divides into unequal parts in the same manner as in the eighth division, and the two teloblasts at the same time move slightly apart. The interspace is occupied by one or two clear, very thin cells, the position of which is clearly shown in the figures, and which I shall describe hereafter. Shortly after this division the products of the two outer teloblasts also divide, one of them transversely, the other longitudinally. In the very perfect preparation figured in Figs. 66 and 76 the four spindles were perfectly symmetrical.

Later divisions. Beyond this point I cannot certainly enumerate the divisions, though I have little doubt that Figs. 67,

68, represent the thirteenth. The residual teloblasts continue to divide in the same manner for some time, but finally break up into small cells indistinguishable from the remaining cells of the ventral plate. The latest stage in which I could certainly distinguish them is shown in Fig. 70, but in considerably later stages (Figs. 81, 82) a group of larger cells can still be seen on either side, which is probably the product of the teloblast, and marks the site of its disappearance. *During these divisions the residual teloblasts move apart so as to leave a triangular space between them covered with small transparent cells (dor), and at the same time they gradually recede from the prototroch towards the lower pole.* This change of position in the teloblasts is of fundamental importance, since I believe the triangular area to represent the middle dorsal region of the adult body, and the residual teloblasts to mark the posterior limit of the ventral plate. *Under this interpretation, therefore, the recession of the teloblasts towards the lower pole represents the shifting or bending of the antero-posterior axis of the larva towards its definite position in the adult body.* This view is fully discussed at p. 431.

With the disappearance of the teloblasts the history of the first somatoblast may be said to close, and I will here only call attention to the side and ventral views of the various stages shown on Pl. XIX. The later history of the ventral plate will be briefly touched upon further on, but I shall defer to a future paper an account of the histological differentiation.

The following diagram gives a general view of the divisions up to the disappearance of the residual teloblasts: —



2. *The Second Somatoblast. Origin of the Mesoblast-bands.*

We may now return to the end of the spiral period of cleavage (Fig. 29) and follow the history of the second somatoblast (*M*). Its mode of formation is shown in Fig. 47 (Pl. XVII). The spindle, which lies in the granular portion of the macromere *D*, is inclined at an angle of 45° to the second cleavage (median line), and as the somatoblast forms, it is pushed over towards the right so as to lie nearly in the middle line in front of the first somatoblast. As a rule the division is completed before the formation of x^2, but I have seen some specimens in which the two cells were simultaneously formed, and one (Fig. 33) in which the somatoblast was completely separated before the appearance of the x^2-amphiaster. The *first* division of the somatoblast cuts it into two equal parts. These are the primary mesoblasts (*M. M.*, Figs. 49, 50). They are invariably displaced towards the left — probably, as I conjecture, because on the right side (Fig. 48) the second somatoblast abuts against the first and there is less resistance towards the other side.

At the *second* division each of the primary mesoblasts buds forth a small cell at the surface, near its anterior margin (Figs. 53, 72. The lessened diameter of the cells in the former figure is owing to their rounding out; in their quiescent state they are considerably flattened against the entomeres). Examination of many specimens shows that there is a good deal of variation in the direction of the spindles, and I found two specimens in which one of the spindles was longitudinal, the other exactly transverse. The budding of the mesoblasts is continued in the same way for a considerable period, until a group of small cells is formed, which lie superficially and form the posterior lip of the blastopore (Figs. 54–57, 73). They become continuous with the anterior cells of the ventral plate, but, as has been already mentioned, they can usually be distinguished from the x-cells, even before the appearance of the pigment, by the granular appearance of their nuclei.

Through this process and by the forward growth of the x-cells, the primary mesoblasts are soon covered in, and lie quite beneath the surface. At the same time the blastopore closes in completely (by a process to be described later). A longitudinal (actual) section through this stage (passing slightly to one side

of the median line and showing two of the entoblast nuclei) is shown in Fig. 88, XX. There is no segmentation cavity, and the entomeres are everywhere closely surrounded by the one-layered ectoblast. The section shows the exact relations of the primary mesoblast (*M*) to the cells of the ventral plate (*v.p.*). Just anterior to the primary mesoblast is a crowded group of cells, some of which lie below the surface and *some of which contain bluish-black pigment-granules*. This group of cells are certainly in part the offspring of the primary mesoblast and form the beginning of the pigment-area (*p.a.*) which has so great a significance in the later history of the larva. These cells I shall call the *secondary mesoblast*. Close examination shows a distinct line of demarcation between the secondary mesoblast cells and those of the ventral plate, but this boundary is not so distinct as it afterwards becomes.

The primary mesoblasts continue to bud forth secondary mesoblast cells for some time after their enclosure. At length, however, the budding ceases and the mesoblasts divide longitudinally into two somewhat unequal parts (Figs. 61, 63), of which the two mesial cells are the larger. By subsequent divisions of the same character (Figs. 77–82) *each primary mesoblast gives rise to a group of cells that extends upwards on each side along the cleavage-line between the anterior and posterior pairs of entomeres*, i.e. *along the line of the first cleavage and at right angles to the prototroch. These two groups of cells are the foundations of the mesoblast-bands, which have, therefore, from the beginning a position at right angles to the margins of the blastopore; i.e.* at right angles to their direction in *Lumbricus, Clepsine*, and *Rhynchelmis*.

Meanwhile the pigment-area increases in size and becomes very distinctly marked off from the surrounding cells (Figs. 79–82, XIX). The pigment is at first arranged in two somewhat V-shaped masses (Fig. 79), but in later stages these become more or less completely connected together and surrounded by scattered granules that occupy a fairly-well defined circular area at the lower pole of the trochophore. *The paratroch is subsequently developed around the margins of this area* (Figs. 85, 90), *and still later the anus appears in the centre of the paratrochal ring. Hence the pigment-area represents the posterior extremity of the adult body.*

I have made many actual sections through the pigment-area which clearly show the structure of the mesoblast-bands, but I figure an optical section (Fig. 70), since it shows much better the relations of the parts. The sections show that the cells of the mesoblast-bands (*m.b.*) are perfectly continuous with those of the pigment-area, from which they are no longer to be distinguished in size. The pigment-cells extend to the surface and might be described with Salensky or Kleinenberg as forming a part of the ectoblast. They are, however, sharply differentiated from the cells of the ventral plate (*v.p.*), not only by the presence of the pigment-granules, but also by a distinct line of demarcation, and the cells do not take the color (Schneider's acetic carmine) in quite the same degree.

In this paper I shall treat very briefly of the later history of the mesoblast, since I wish to leave this to a second paper. I will therefore give only such a brief sketch of the leading facts as will serve to connect the embryonic topography with the larval and adult bodies. The pigment-area remains distinct until the elongation of the body has made considerable progress (Figs. 85–89) and the mesenteron has acquired a small cavity. The pigment-cells then migrate inwards (Figs. 90, 91) and spread out upon the wall of the mesenteron, where their nuclei and outlines can easily be seen in entire specimens mounted either in glycerine or in balsam. Every stage in this progressive migration may easily be seen, and as the cells pass inwards they disappear correspondingly from the surface, though one or two small pigment-spots remain until a rather late period. The anus is finally formed in the middle of the area formerly occupied by the pigment-cells.

I have not yet fully investigated this process by means of section, and hence must speak of it with some reserve. It is possible to suppose that no actual inward migration takes place, and that the appearance is caused by the successive development of pigment in the inner cells and its concomitant disappearance from the outer. All the appearances, however, speak for an actual migration of the cells, and actual sections of the earlier stages show the cells of the pigment-area much elongated, often with the bodies of the cells lying below the surface, with long pointed ends directed outwards.

The longitudinal muscles (*l.m.*, Fig. 85) are differentiated at

a relatively early period, before the inward migration of the pigment-cells. For this and other reasons it is nearly certain that they arise from the mesoblast-bands, *i.e.* from the progeny of the primary mesoblasts after the pigment-cells have been budded forth. They form, at first, a small loose bundle on either side dorsal to the seta-sacs, whence they extend themselves over the dorsal region. The remaining differentiations of the mesoblast I shall consider hereafter.

3. *History of the Second and Third Groups of Micromeres.*

The last points to be considered in the embryonic development relate to the general history of the second and third groups of micromeres, including the formation of the stomodæum and the general relations of the blastopore. It will be convenient to begin with one of the middle stages, and to consider the earlier history afterwards.

At a stage shortly before the closure of the blastopore, three cells are always found, symmetrically disposed about the lips of the blastopore; these cells I have called the *stomatoblasts* (*st.*, Fig. 56, Pl. XVII), since from them the stomodæum is in large part, perhaps wholly, derived. One of them (*st.m.*) lies in the middle line in front, wedged into the cleavage-line between *A* and *B*. The other two (*st.r.*, *st.l.*) lie, one on either side, opposite the cleavage-lines between *B* and *C*, and *A* and *D* respectively. These cells are easily distinguishable from the surrounding cells, not only on account of their size, but also because they appear (perhaps on account of their thickness) somewhat darker and more granular than the others.

These cells have certain constant and characteristic relations to the surrounding cells, which are shown in Diagram No. IV. The space between the median and the left stomatoblasts is occupied by a group of smaller cells, most of which, at any rate, are the products of a^3 (the left anterior micromere of the third group). The corresponding space between the median and right stomatoblasts is in like manner occupied by the progeny of b^3 (the right anterior micromere of the third generation). The posterior lip of the blastopore, as has been shown, is formed by the secondary mesoblast-cells, budded forth from the primary mesoblasts. Wedged in between them and the left stomatoblast

is invariably found a larger cell (Figs. 55 to 57), that I for a long time mistook for a product of the primary mesoblast, but which is unquestionably d^3 (the left posterior micromere of the third group or one of its progeny), as will be shown later. Corresponding to it on the other side, adjacent to the right stomatoblast, is c^3 (the right posterior micromere of the third group), and between this and the secondary mesoblast-cells is a cell which I believe to be one of the progeny of x^1. It will be

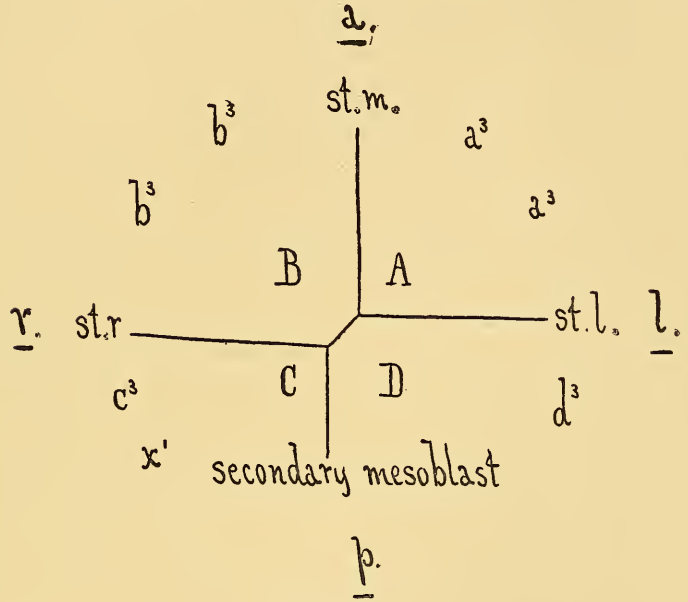


DIAGRAM IV.

observed that the margin of the blastopore is not quite symmetrical, since it includes one of the x-cells on the right side. This curious asymmetry is, I believe, quite constant, and appears to be caused simply by the displacement of the second somatoblast towards the left, so as to come into juxtaposition with d^3 and *st.l.* (Fig. 53), and thus separate x^2 from the blastopore. It is by the convergence of this circle of cells that the blastopore closes; and, before taking up the rather complicated phenomena involved in the closure, I will endeavor to trace the origin of the cells in the cleavage. The condition of the blastopore at the end of the spiral period has been described

at p. 404, and I refer again to Diagram III, which shows its marginal cells (*cf.* Figs. 25, 26, 31, 33, 36, 47 to 48 : it will of course be understood that in such a Mercator's projection some distortion is inevitable, which appears mainly in the excessive size of a^3, b^3, c^3, d^3). It will be observed that $a^{2.2}$, $b^{2.2}$, and $c^{2.2}$ lie opposite the respective cleavage-lines between the macromeres, — a point of importance in the subsequent orientation. As the closure of the blastopore proceeds, $a^{2.1}$, $b^{2.1}$, and $c^{2.1}$, which from the first lie somewhat outside the others, are, as I believe, left entirely behind, so as to form no part of the blastopore-margin; whereas the other cells are pushed downwards, and their descendants form the lip of the blastopore, as shown in the Diagram IV. To substantiate this statement I shall be obliged to describe the history of the cells somewhat in detail by returning to an earlier period. I have shown that, in the course of the fifth cleavage, the secondary micromeres (a^2, b^2, c^2) divide somewhat unequally, in a left-handed spiral (as seen from above), the larger cell ($a^{2.1}$, $b^{2.1}$, $c^{2.1}$) in each case lying somewhat above the other and in contact with the girdle-cells (Figs. 25, 26, 33, III). In their later divisions (Figs. 36, 45) the upper cells divide vertically, so as to give rise to a series of large polygonal cells, lying below the prototroch ; these I shall call the *post-trochal cells* (*cf.* Figs. 75, 76). It is between these cells and the entomeres that the head-kidney takes up its definitive position and begins to elongate. They are clear, show a marked tendency to vacuolation, and it is these cells that I have suggested at p. 403 may possibly be comparable with the velar or external excretory organ of the molluscan veliger.

Meanwhile the smaller or lower cells ($a^{2.2}$, $b^{2.2}$, $c^{2.2}$) also divide, but in a different manner. The first division is horizontal (more or less oblique) and also unequal, a smaller cell being budded off above, next the prototroch. That this takes place in all of three of the cells in the same manner, I only infer from their later arrangement ; but I have several times observed the actual division, in the manner described, in $c^{2.2}$, and it seems fair to conclude that it holds for the others also. The first divisions of the third group of micromeres (a^3 to d^3), which meanwhile take place, are also horizontal (*cf.* Figs. 49, 50, 53).

We have now arrived at a stage, however (Figs. 52 to 55), where $c^{2.2}$ *and* $a^{2.2}$ *can with certainty be recognized as the right and*

left stomatoblasts respectively. I cannot state as positively that $b^{2.2}$ is the median stomatoblast, but I have no doubt that such is the case. The first division of c^3 and d^3 is shown in Fig. 50, and the connection between this and our starting-point (Fig. 55) is given by Figs. 53 and 54.

4. *Closure of the Blastopore. Formation of the Stomodæum.*

The blastopore now rapidly closes by a convergence of all these cells towards a central point, which lies slightly anterior to the lower pole, usually about the middle of the cross-furrow. The convergence of the cells, which is rather sudden, is brought about by a very interesting process, which has superficially the appearance of an embolic gastrulation. A marked depression appears around the lower pole, bounded in front and at the sides by the stomatoblasts and the small cells between them, and behind by the cells immediately covering the primary mesoblasts. This is shown from the lower pole in Figs. 62, 63, XVII, in side-view in Fig. 77; and the same embryo is shown in optical section in Fig. 78. The depression now rapidly disappears and the embryo again becomes perfectly spherical (as shown in actual section in Fig. 88, XX). This is not caused, however, by a bending out of the walls, but by a *drawing together or convergence of the cells towards a central point*, at which a distinct pore is for some time left (see Fig. 79). The stomatoblasts meanwhile divide radially, and by the curious process just described they are drawn together so as to form an arc of cells, just behind which appears the pore (Fig. 79). The small cells that occupied the floor of the depression are meanwhile crowded together and entirely change their form. Hitherto they have formed a thin pavement-epithelium over the floor of the depression. Now they are squeezed together until they assume a narrow, prismatic form, and form a kind of plug (*cf.* Figs. 78, 88) between the stomodæal arc and the primary mesoblast-cells (immediately internal to which lie the entoblast-nuclei). *The pigment appears in the cells of this plug on either side the pore as the convergence takes place, and a comparison of the figures shows from their position that they must be, in large part at any rate, the secondary mesoblast-cells.*

It is an extremely important question, but one well-nigh

impossible to decide with certainty, what is the fate of the small cells (the products of a^3 and b^3) that lie between the stomatoblasts, before their convergence. Do they pass into the pigment plug with the secondary mesoblast-cells, and if so, do they migrate inwards with them to form a part of the mesoblast? Here we have, as I believe, the only possibility in the development of *Nereis* that the mesoblast may arise from the ectoblast in Salensky's and Kleinenberg's sense. Unfortunately I cannot give a definite answer to this question. But after studying a large number of favorable surface-views (in which the history of the cells can be traced much better than in section), it is my belief that they do not pass inwards, for the following reasons: First, some of these cells certainly become wedged in between the large stomodæal cells as they converge, while others remain as a group of unpigmented cells that lie between the pore and the stomodæal arc (Figs. 79, 80, which accurately represent the cells as far as they are visible). This group of cells (as shown in Fig. 80) is enclosed by the stomodæal arc in later stages, and thus still more definitely separated from the pigment-area, and it is certain that if any contribution is made by these cells to the mesoblast, it must be of minimal amount.

The stomodæal arc rapidly enlarges by radial divisions of its cells (Fig. 80) and is soon converted into a circle with a small opening in the middle which forms the mouth (Fig. 81). The cells at the same time assume a columnar or wedge-shaped form and are partially overgrown by the neighboring small cells, so as to reach the surface only at the lips of the mouth-opening (*cf.* Figs. 82, 84, 88). Meanwhile a group of cells (*s.g.*) arises on either side the stomodæum (undoubtedly derived from it), which in later stages forms a pair of glandular masses (?) lying at the junction of the stomodæum (pharynx) and the mesenteron (Fig. 92). These may be called the *stomodæal glands.*

I will finally call especial attention to the fact that upon the demarcation of the pigment-area, which takes place at the same time as the completion of the stomodæum, it lies in immediate juxtaposition to the latter (Figs. 81, 82). The pigment-area, however, marks the posterior end of the adult body, *and hence*

the median ventral line of the adult body does not yet exist. Mouth and anal area arise side by side in the region where the blastopore closes, though the anus does not break through until they have been widely separated.

In the meantime the remaining descendants of a^3, b^3 extend themselves over the anterior and lateral regions, between the stomodæum and the prototroch. The smaller cells budded off from the median stomatoblast, and also the descendants of $b^{2.1}$ become indistinguishably intermingled with them. From this group of cells arises the ectoblast surrounding the stomodæum and forming the superficial part of the body-wall of the antero-lateral region. The postero-lateral region on each side (between the margins of the ventral plate and the prototroch) is occupied by the descendants of the post-trochal cells (offspring of $a^{2.1}$ on the left side and of $c^{2.1}$ on the right) and of c^3 and d^3. These cells are continuous behind with the small cells that separate the posterior teloblasts from the prototroch; *i.e.* the descendants of x^3 and (?) of x^6, x^6 (see p. 410). *From the latter, as I believe, arise the cells that occupy the triangular area between the two residual teloblasts after their divergence. This area afterwards forms the middle dorsal region of the trunk.*

The line of parapodia may be taken to represent the lateral region of the adult body on each side. Now, the seta-sacs (which mark the position of the parapodia) are developed from the ventral plate. *Hence the cells lying above the ventral plate on each side* (i.e. *the descendants of the post-trochal cells*) *form the lateral portion of the dorsal region of the trunk.* (This conclusion will be rendered clear by referring to the discussion of the axial relations, with the accompanying diagrams, at p. 426.)

With this my account of the cleavage closes. The general relation of the primary blastomeres to the larval and adult bodies are shown in the following table:—

Entomeres.	Mesomere. Second Somatoblast.	First Group of Micromeres.	Second Group of Micromeres.	Third Group of Micromeres.
Mesenteron.	Mesoblast-bands.	1. Prototroch. 2. Apical organ. 3. Head-kidneys. 4. General ectoblast of the upper hemisphere. 5. The cross and the cerebral ganglion.	*a*. The first somatoblast. Ventral Plate. 1. Ventral nerve-cord. 2. Seta-sacs. 3. General ectoblast of post-oral ventral, and lateral regions. 4. Portions of the nephridia(?) 5. Ectoblast of the middle dorsal trunk-region. *b*. The three smaller micromeres (a^2, b^2, c^2). 6. The stomodæum. 7. Portions of the circum-oral general ectoblast. 8. The post-trochal cells. Ectoblast of the lateral dorsal trunk-region.	Portions of the general ectoblast of the circum-oral and circum-anal regions.

VII. General History of the Metamorphosis.

As a considerable time may elapse before the publication of the second part of this paper, it seems desirable to give a sketch of the structure and metamorphosis of the larva in order to make clear its rather peculiar relations to the adult body and to justify my orientation of the early stages.

After the disappearance of the ventral depression the larva becomes perfectly spherical, and this form is retained up to the time when the stomodæal arc closes (a stage slightly later than Fig. 80, 18 hrs.). After the occurrence of this event the lower hemisphere begins to change its shape, becoming slightly flattened in front (Fig. 82), so that the most prominent point is somewhat behind the lower pole, which lies about in the centre of the pigment-area. As this marks the first step in the metamorphosis, the general structure of the larva at this stage may be briefly described. The entomeres are still undivided and

retain their original arrangement (*cf.* Fig. 86). They are everywhere closely surrounded by the ectoblast except at the sides, where the mesoblast-bands intervene (Fig. 81). The prototroch encircles the equator of the embryo; the mouth lies in the median ventral line about half-way between the prototroch and the margin of the pigment-area. There is no post-oral band of cilia, and no ventral ciliated area. The prototroch shows the usual interruption in the median dorsal line. On the upper hemisphere a pair of eye-spots have appeared, the position of which may be seen by a comparison of Figs. 82, 85, 86. On the anterior half of the upper hemisphere are five spherical bodies arranged in a regular arc, one of them lying in the median line, the others symmetrically placed on either side of it. These bodies, which I at first mistook for sense-organs, I shall call the *frontal bodies*. Each of them appears to be developed out of a single cell, in which appears a clear space like a vacuole surrounded by a layer of granular protoplasm. The clear space stains intensely with hæmatoxylin precisely like the contents of the gland-cells that occur so commonly in the larvæ of other annelids (*e.g.* in *Spirorbis* or *Terebella*); and from this fact and from their later history I am led to regard them as glands. It will be shown further on that these bodies are of great importance in the orientation of the larva, since *they mark the anterior extremity*.

The ventral plate (Fig. 81) is composed of crowded prismatic cells. Posteriorly it ends in two distinct groups of cells (*X*, Figs. 81, 82), which I believe to be the last traces of the residual teloblasts. These groups of cells are separated from the prototroch on each side by a lateral area and from each other by a median triangular area, over which the cells are very thin and delicate and show a marked contrast to those of the ventral plate. The triangular area represents the median portion of the dorsal region, the lateral areas the lateral portions of the dorsal region of the adult body. The relations of these regions to the cleavage-blastomeres have been already given.

There is still no sign of metamerism or of a body-cavity. On the upper hemisphere the ectoblast shows distinctly the beginning of the supra-œsophageal ganglia in the form of a broad transverse thickening of the ectoblast (neural plate), narrower in the middle, and extending down on either side to the prototroch. The central part bears the apical tuft of cilia, still in

full activity. The approximate outlines of the neural plate are shown by the dotted lines in Fig. 86, but there is no distinct boundary, the neural plate being indicated only by the greater depth of the cells and by their smaller size.

The head-kidneys now completely surround the body in the position shown in Fig. 82.

At this period the larvæ swim very actively, in the usual manner, rotating about the vertical axis and exhibiting a very marked heliotropism.

From this time forward I shall employ a different set of terms in the orientation (see p. 426 for the grounds on which this procedure is based). I shall designate the site of the frontal bodies as the anterior extremity, the centre of the pigment-area as the posterior, the flattened (anterior) side of the lower hemisphere as ventral, and the opposite side as the dorsal.

The general character of the metamorphosis is shown in Pl. XX. The body gradually elongates in an axis that coincides with the original vertical axis (*i.e.* at right angles to the prototroch), the pigment-area being carried away from the mouth and remaining at the posterior end of the body. Meanwhile the cells of the ventral plate grow inwards from each side towards the middle line between the pigment-area and the stomodæum, which are thus forced apart; and in the space thus formed the two halves of the ventral plate undergo a regular process of concrescence along the median ventral line, where a distinct seam may for some time be seen in the surface-views (Figs. 83, 87). The origin of the median ventral region may thus be followed step by step — almost cell by cell — from the beginning. On either side the line of concrescence appears a distinct thickening, the ventral neural plate, from which arises the ventral nerve-cord. Thus the ventral cord arises from two separate halves which have at first no connection with the cephalic neural plate.

As the elongation begins, the seta-sacs make their appearance, and with them is given the first indication of metamerism. Those of the first two somites appear first (Figs. 83, 84), the dorsal and ventral rami being represented each by a somewhat vague rounded mass of cells. Those of the third somite appear somewhat later (Fig. 85), about the same time with the differentiation of the longitudinal muscles. At the same time the

setæ appear in the two anterior pairs, and the paratroch (*par.*) appears around the margin of the pigment-area.

The setæ are protruded from the two anterior pairs of seta-sacs about the fortieth hour (Fig. 89), the others not until a considerably later period. This is followed by the appearance of the parapodial cirrhi in the second and third somites (they are never developed in the first), and at the same time two incomplete mesotrochal bands of cilia appear (Figs. 90, 91) at the posterior margin of the first and second somites respectively.

From this time forwards the body rapidly develops into the adult condition. About the sixtieth hour (Fig. 91) the anal cirrhi (*a.c.*) make their appearance inside the paratrochal ring; at the same time the cephalic tentacular cirrhi (*t.c.*) appear, *posterior to the prototroch*, two new pairs of eye-spots are developed, and the setæ of the third somite are put forth. The somites become distinctly marked off, the parapodia become prominent, and the larva now possesses a distinct head and a trunk consisting of three somites.

Certain other details in the larval development demand a brief mention. Towards the fortieth hour (or earlier) a granular reddish-brown pigment appears in the cells adjoining the large prototrochal cells, and to some extent in the peripheral portions of the ciliated cells themselves. The large ciliated cells are thus rendered extremely conspicuous (Figs. 89, 90), and may easily be counted in the living larvæ. The pigment is very irregularly distributed, and varies extremely in different individuals. It is moreover changeable in the same individual, for a sudden disturbance seems to cause a contraction either of the pigment-cells or of the pigment-granules (chromatophores?). I have often observed finely pigmented specimens swimming in a watch-glass, which when brought under a cover-glass (still actively swimming) at once became nearly colorless. As the animal grows older, the girdle of pigment becomes broken up into irregular patches, two of which, one on either side the head, usually persist until a late stage (*cf.* Fig. 92). Ultimately, however (fifteen days), the pigment disappears.

About the sixtieth hour (Fig. 90) a number of peculiar sense-hairs appear at the anterior and posterior extremities. Anteriorly there is a group of about seven short, stiff, knobbed hairs on the apical region (Fig. 90) (the apical cilia have disappeared).

In the perianal area a long, stiff flagellum (*a.f.*) appears in the middle line, and on either side of this one or two knobbed hairs, like those of the apical region. As the anal cirrhi grow forth, these knobbed hairs are borne at their tip (Fig. 91), where they remain up to the latest stages I have observed. In connection with these sense-organs, mention may also be made of a series of pigment spots that appear on either side of the latero-dorsal surface, about the middle of each somite.

In the three-segmented stage, the larva remains for a relatively long period (about twelve days), during which the only important external changes concern the development of the head (Fig. 92).

In the first place, the head changes its form, becoming at first flattened (Fig. 91) and afterwards elongated, *the frontal bodies being borne at its anterior extremity*, while the prototroch becomes interrupted above and below, so that only two lateral tufts of cilia remain. At the same time the head becomes distinctly marked off from the trunk-region by *a constriction that lies immediately anterior to the first pair of parapodia, and posterior to the tentacular cirrhi, and therefore in the lower hemisphere of the trochophore.* At a later period, a distinct segment-line encircles the body at this point (Fig. 92), and the head is completely marked off. The mouth lies far anterior to this and in front of the tentacular cirrhi, and there is no trace of a division between the head and a mouth-segment ("mund-segment"). The mouth-segment, therefore, belongs to the unsegmented part of the body, and arises morphologically as a differentiation of the head, — a result in entire accordance with my studies of *Lumbricus*. It is to be observed, further, that to the head-region belongs, not only the upper hemisphere, but also the prototroch and a portion of the lower hemisphere.

Meanwhile the frontal bodies undergo certain changes of form and finally disappear. They are at first spherical, but afterwards assume a pear-shape, the clear space extending out into the narrower portion, which is perhaps to be regarded as a kind of duct. At first separated from each other, they are later brought into contact, crowded closely together, and, after diminishing in size and becoming distorted in form, they disappear in the surrounding ectoblast.

Meanwhile the tentacular cirrhi grow out into long, slender

appendages (Fig. 92). A pair of frontal antennæ (*f.a.*) grow forth from the apical region, and a third pair of appendages (*pl.*) make their appearance just in front of the mouth. The latter differ in form in the two species, being slender and pointed in *N. megalops*, but blunt and rounded in *N. limbata*. These appendages I take to be the "palpi." They, like the antennæ and cirrhi, bear a number of knobbed sense-hairs, some of which are also found on the surface of the head itself. A pair of pigment-spots also appear on the lower side of the head.

On the upper side of the head, the supra-œsophageal or cerebral ganglia appear as an enormous bilobed thickening of the ectoblast. They are distinctly posterior to the frontal antennæ, which extend straight forwards from the anterior extremity of the body. Now, the "frontal bodies" are last seen in the interval between the bases of the developing frontal antennæ; *i.e.* they also are at the anterior extremity. In the spherical trochophore, however (Figs. 84 to 86), *they lie in front of the cephalic neural plate, and in front of the upper pole. The upper pole of the trochophore, therefore, does not coincide with the anterior extremity, but lies in the dorsal region.*

The history of the alimentary canal may be briefly dismissed. As the body elongates, the stomodæum changes its form, becoming finally drawn out until it reaches the middle of the first somite (Figs. 91, 92). The jaws appear within its cavity about the fourth day. Meanwhile the mesenteron acquires a cavity, which appears as a central space between the entomeres. I need not describe the origin of the alimentary epithelium, as this has been carefully studied by Salensky and v. Wistinghausen; but I may call attention to the history of the oil-drops. In the undivided egg there are from ten to twenty of the large oil-drops. As the segmentation proceeds, the drops in each macromere gradually fuse, until only one drop is finally left in each. The four oil-drops are arranged in two pairs, the anterior of which, contained in the anterior entomeres (*A* and *B*), are much smaller than the others. Since the drops do not change their position with the movements of the embryo, they form an admirable means of preliminary orientation, both in living and in preserved specimens. The oil-drops persist long after the appearance of the mesenteric cavity (Figs. 90, 91), but are finally absorbed. The development of the proctodæum I have not yet fully investigated (see Salensky).

I may call attention finally to the frequency with which the three-segmented larva occurs among annelids, — a fact which almost tempts one to compare it with the Crustacean *Nauplius* or the three-segmented Pycnogonid larva. In *Nereis* the three segments are well developed by the middle of the third day, while the fourth segment does not appear until about the twelfth day. During the whole of this period the larva continues to swim, though latterly much less actively than at first. The same pause after the appearance of the first three segments takes place in many other forms, and it is not easy to avoid the conclusion that this curious analogy with the *Nauplius* is more than accidental.

VIII. Axial Relations of the Nereis Trochophore.

The axial relations of the *Nereis* larva are of great interest and seem to afford new evidence on a number of important questions. At first sight they appear to present a number of features which are irreconcilable with those of the typical trochophore (*e.g.* of *Polygordius*). When carefully studied, however, these peculiarities are found not only to be easily explicable, but even to afford new data for a consideration of the axial relations of the trochophore in general. In the fully established trochopore (Diagram V, *A*, *B*) the mesoblast-bands (dotted) extend straight forwards from the pigment-area (*p.a.*), at the centre of the lower hemisphere, at right angles to the plane of the prototroch. The subsequent elongation of the body takes place in the direction of the mesoblast-axis, *m*; *i.e.* parallel to the mesoblast-bands; and the anus is formed in the centre of the space originally occupied by the pigment-area. *The pigment-area, therefore, represents the posterior extremity of the adult body.*

Thus far the larva agrees precisely with the typical trochophore of *Polygordius*, *Eupomatus*, or *Hydroides*. As soon, however, as the ventral plate is considered, we encounter an apparent contradiction. For the neural axis, *n* (which coincides with the long axis of the ventral plate, of which the neural plates form a part), is *parallel* to the prototroch, and hence *at right angles to the mesoblast-axis*. For reasons given at p. 436, it is impossible to doubt that the posterior teloblasts of *Nereis*

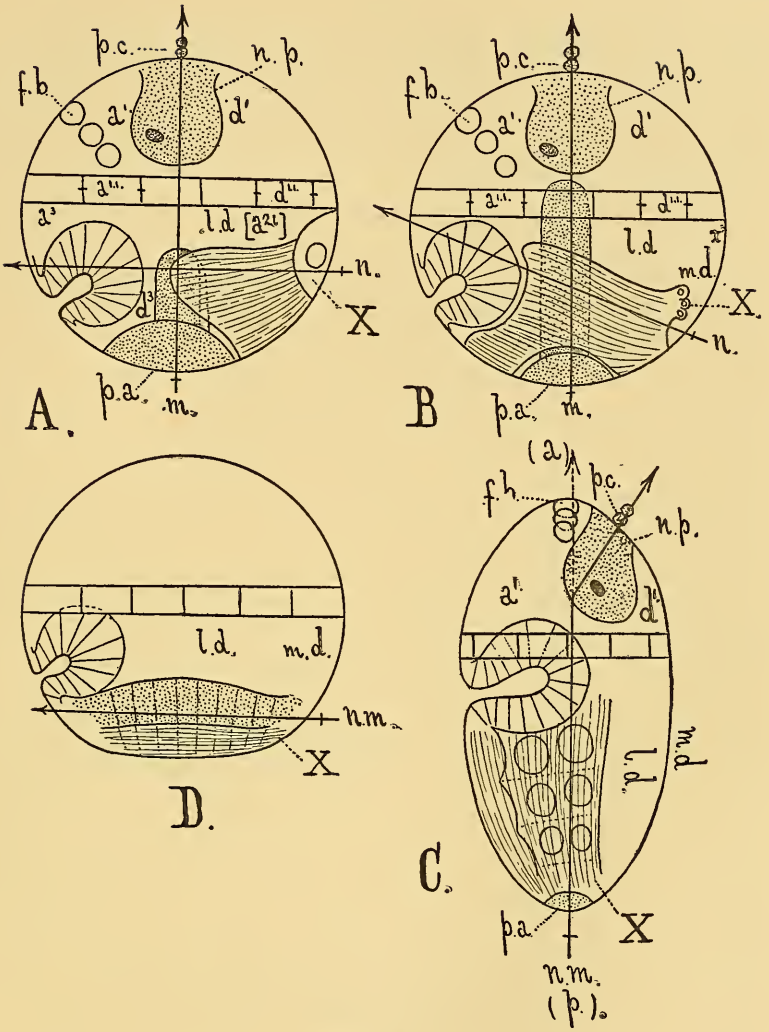


DIAGRAM V.

A. Early trochophore of *Nereis* from the left side; a^1, d^1, a^3, $a^{2\cdot1}$, $a^{1\cdot1}$, $d^{1\cdot1}$, x^3, regions derived from the corresponding micromeres; *f.b*, frontal bodies; *l.d.*, latero-dorsal region; *m.d.*, median dorsal region; *m.*, mesoblast axis; *n.*, neural axis; *n.p.*, cephalic neural plate; *p.c.*, polar cells; *p.a.*, pigment-area. The cephalic neural plates, the pigment-area, and the mesoblast bands are stippled; the ventral plate (product of *X*) shaded with lines. The dark body is the eye-spot.

B. Corresponding view of later stage. Beginning of the shifting of the neural axis. Concrescence of the ventral neural plates.

C. Diagram of the three-segmented larva (adult condition). Completion of the axial shifting, coincidence of the neural and mesoblast axes. Shifting of the frontal bodies and of the cephalic neural plates.

D. Young larva of *Lopadorhynchus* from the right side, before the shifting of the axes.

(*X*) are the homologues of the neuro-nephroblasts of the Hirudinea and Oligochæta, which lie at the posterior extremity of the germ-bands. The position of these teloblasts in *Nereis* must, therefore, also mark the posterior extremity; yet they lie in contact with the prototroch, ninety degrees away from the centre of the pigment-area.

This curious discrepancy appears at first sight to be a fatal blow for the "Achsenzoologen." It appears to me, however, simply to demonstrate the truth of the view urged by Hatschek and others that a shifting of the axes takes place in the course of the metamorphosis. The discrepancy is due in *Nereis* simply to the fact that the mesoblast axis and the neural axis do not shift at the same time. The former takes up its definitive position much earlier than the latter, so that the larva passes through a transitional period in which the two axes form an angle with each other (*B*). I think it will be easy to show that *the precocious shifting of the mesoblast-axis is caused by the early concentration of the material of the ventral plate in the first somatoblast.* To establish this proposition will require some consideration of the gastrulation and trochophore-formation in other annelids.

It may, I think, be taken as a well-established fact that throughout the trochopore series (Annelida, Mollusca) the blastopore occupies primarily the central portion of the lower hemisphere ("Gegenfeld"), and its margins are parallel to the plane of the prototroch, which is often well developed long before the close of gastrulation. The mesoblast-bands arise from cells (usually, perhaps in the last analysis always, a single pair of teloblasts) that lie symmetrically in a definite position at the lip of the blastopore (Diagram VI, *A*). These cells define not only the median plane, but also the posterior region of the embryo, and by almost all writers this portion of the blastopore-margin is designated as the posterior lip. The closure of the blastopore typically proceeds forwards from the posterior lip, in the direction of the arrow, its anterior portion usually persisting as the mouth, or marking its position. During, or sometimes before, the process of closure the mesoblast-cells pass into the cleavage-cavity, where they ultimately give rise to the mesoblast-bands.

Among the annelids the axial relations of the mesoblast-bands (and also of the neural bands) with reference to the blastopore are of two types. (1) *In the first type, typically represented by*

Lumbricus (Diagram VI, *B*) *and in a modified form by Rhynchelmis and the Hirudinea, the primary mesoblasts remain in their original position, the mesoblast-bands are parallel to the original lips of the blastopore, and the embryonic mesoblast-axis persists in the adult.* The same is true of the neural axis; for the neural bands are parallel to the mesoblast-bands, forming with the latter the principal basis of the so-called germ-bands.

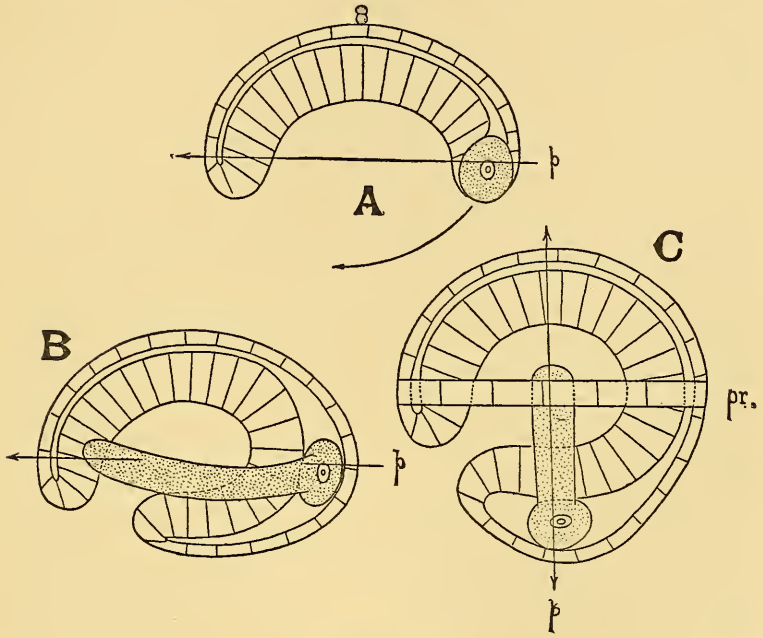


DIAGRAM VI.

A. Early annelidan gastrula. The mesoblast is shaded.
B. Horizontal type of the fœtal form (*Lumbricus*).
C. Vertical type of the larval form (*Polygordius*, etc.).

For the evidence on which this statement rests I refer to my paper on *Lumbricus* (No. 29) and to the well-known researches of Whitman and Vejdovsky.

(2) *In the second type, represented by the Polychæta in general* (Diagram VI, *C*), *the primary mesoblasts or their equivalents are sooner or later carried downwards until they lie approximately at the centre of the lower hemisphere. The mesoblast-bands are therefore at right angles to the lips of the blastopore;* i.e. *the*

mesoblast axis is rotated through 90°. The same is true of the neural axis.

The truth of this statement becomes at once apparent on considering the development of *Lopadorhynchus*, where the rotation of the axis is effected very late in the development. In the young lava (Diagram V, *D*) the mesoblastic and neural bands are horizontal and parallel to the prototroch (*cf.* Kleinenberg, No. 14). In the course of the metamorphosis both are gradually rotated by the downward growth of the dorsal region (*l.d.*, *m.d.*) until they are at right angles to the prototroch, *always*, *however*, *remaining parallel to each other; i.e.* the shifting of the neural and of the mesoblastic axes takes place at the same rate. I call special attention to the fact that the rotation of the axis is not ideal, but actual; it is caused by the more rapid growth of the dorsal region, which as it were swings the whole ventral plate into place. In *Eupomatus* the process is somewhat obscured owing to the early differentiation of the primary mesoblasts and to the fact that the mesoblast-bands are not formed until after the axial shifting has taken place. Moreover, the precise history of the neural plate has not been made out. When these facts are taken into account, however, a study of Hatschek's figures shows that the axial relations agree essentially with *Lopadorhynchus.*

Viewed in the light of these comparisons the axial relations of *Nereis* are easily intelligible. The primary mesoblasts, as usual, lie at the posterior lip of the blastopore, and a comparison of the various figures (*e.g.* 34, 51, 56) will show that during the closure of the blastopore they are shifted somewhat downwards and forwards, as is proved by their position with reference to the cross-furrow. The actual change of position is, however, very slight, since, as the figures show, *the mesoblast* (*second proteloblast*) *is from the first prevented from occupying its usual position by the huge mass of the first somatoblast.* It is accordingly segmented off from the macromere in nearly its definitive position.[1]

The shifting of the mesoblast-axis is in fact brought to pass primarily by the rotation of the cleavage-spindle (*i.e.* the plane of division), by which the somatoblast is separated from the

[1] The justice of this statement will, I think, be realized after an examination of Figs. 47 to 50. *XVII.*

entoblast, and only secondarily by the subsequent displacement of its products. This represents the opposite extreme to *Lumbricus*, where the mesoblast retains its original position. *Lopadorhynchus* occupies a middle ground. The series seems to me an interesting example of the reaction of external mechanical conditions on the form of cell-division.

The problem of inheritance which it involves is touched on in a following passage.

We may now briefly consider the ventral plate. The essential points in its history are as follows: At first the entire material of the ventral plate (first somatoblast) lies in the median line, quite behind the mesoblast (V, *A*). By the division of the somatoblast into two, and ultimately into four, equal parts, this material is equally distributed on either side the middle line, though the two halves subsequently become so intimately united along the middle line that they can only be distinguished posteriorly. Finally, as the body elongates, the two halves of the ventral plate grow forward at the sides of the pigment-area (*cf.* Diagram V, *A*, *B*), inwards between it and the stomodæum, and undergo a process of concrescence along the median ventral line, as described at p. 422. The pigment-area meanwhile is carried backwards. (The pigment-area might be said to migrate backwards, virtually cutting its way through the middle of the ventral plate. The primary cause of the change seems, however, to lie in the growth of the ventral plate.)

Meanwhile the shifting of the neural axis takes place. Mention has been made at p. 410 of the recession of the residual teloblasts from the prototroch. This, I conceive, is caused by the increasing development of the dorsal region, which has hitherto remained in a rudimentary state, and it marks the beginning of the rotation of the neural axis, as shown in Diagram V, *B*. I have not been able to follow the recession further than the stage indicated in the diagram; but when the facts of *Lopadorhynchus* are recalled, it is impossible to doubt that the region of the residual teloblasts is ultimately carried down to the region of the pigment-area.[1] The final condition

[1] This view of the axial shifting is essentially in accordance with the earlier view of Hatschek, which he now seems inclined to abandon in favor of the view that it is only the mouth and stomodæum that undergo a change of position (*Zoölogie*, III, pp. 319, 320).

is shown in Diagram V, *C*, where the neural and mesoblast axes practically coincide. It is probable that the actual space between the residual teloblasts and the pigment-area is never obliterated — *i.e.* that the rotation is completed simply by the form of growth as the body elongates. I may point out that in *Lumbricus* also the posterior extremities of the neural and mesoblastic bands are separated by a considerable space. This shows simply that the posterior extremity is not a geometrical point.

We may finally review in a few words the axial history of the upper hemisphere. The facts stated at p. 425 in regard to the frontal bodies and the cerebral ganglia render it nearly certain that the centre of the upper hemisphere lies in the dorsal surface and does not represent the anterior extremity. The polar cells are extruded at this point, where they persist up to a late stage (Fig. 41). There is no doubt that this point coincides with the centre of the cross, and von Wistinghausen's observations on *N. Dumerilii*, in connection with my own, leave little doubt that the centre of the cross coincides with the centre of the cephalic neural plate, from which the cerebral ganglia develop. These ganglia, however, lie behind the anterior extremity (p. 425, and Diagram V, *C*), the position of which is nearly indicated by the position of the frontal bodies. The anterior and posterior extremities are, however, but vaguely defined in the early larva. They, like all the other features of the body, are only gradually marked out as the development goes forward.

IX. Comparison with Other Forms.

1. *Comparison with Other Species of Nereis.*

The works of Götte and Salensky, which have already been briefly reviewed at p. 369, are too fragmentary to afford a satisfactory basis for a comparison of the early stages with the American species, and I shall therefore depend mainly upon v. Wistinghausen. Still, both the former authors observed certain important points which it is desirable to consider.

Götte (*N. Dumerilii*, free-swimming trochophore) figures correctly the first three cleavages, and gives also the true orientation of the embryo. He then describes accurately the formation

of the first somatoblast, from the left posterior macromere. With this, according to his statements, the separation of the germ-layers is completed. The first four micromeres give rise to the entire ectoblast, the somatoblast contains the entire mesoblast, while the four macromeres form the entoblast. I have given, at p. 371, reasons for regarding this account as erroneous. A careful comparison of Götte's figures with those of Salensky, v. Wistinghausen, and my own, renders it practically certain that Götte entirely overlooked the formation of the second and third sets of micromeres (the first somatoblast of course excepted), and of the second somatoblast or primary mesoblast, for which he mistook the first somatoblast. It is impossible to believe that the discrepancy is owing to the difference of species, for reasons already given.

As regards the later stages, I believe Götte's interpretation of the axial relations to be essentially correct. His account of the shifting of the axes, of the origin of the dorsal trunk-region, and of the relations of the upper hemisphere of the larva to the adult head, agree nearly with my own. The one important difference relates to the mesoblast-bands, which Götte describes and figures as horizontal, the mesoblast-axis coinciding with the neural axis and shifting with it. On this point, again, Götte is almost certainly in error, as shown by the united testimony of Salensky, v. Wistinghausen, and myself.

Salensky (*N. cultrifera*, suppressed trochophore) failed to observe the early stages of cleavage. He showed, however, that the ectoblast does not arise simply from the first four micromeres, but is increased by the separation of additional micromeres from the macromeres. He figures with perfect accuracy the two somatoblasts (Fig. 3 *n.*, Pl. XXIII, "*e*" = *X*, "*b*" = *M*) in their relations to each other and to the blastopore, and they agree precisely with the American species. In the succeeding stage (Fig. 3 *n.c*), the fission of the somatoblasts takes place exactly as in our species, the second somatoblast dividing first. The agreement is so precise and detailed that even the cell x^2 is shown ("*c*" in Salensky's figures) in the same position and dividing at the same time as in *N. limbata* and *N. megalops*. Nevertheless, Salensky did not succeed in establishing the connection between these stages and the later ones, and hence, misled by Götte's statements, he is curiously wide of the

mark in his conclusions. He correctly describes the mesoblast as arising by a proliferation of the ectoblast near the posterior lip of the blastopore. This region of the ectoblast, however, he supposed to be derived from two large *superficial* cells (*me.*, Figs. 4 *n.*, 4 *n.a.*, Pl. XXIII; their relations to the cells "*e*" and "*b*" of the last stage were not determined), which he correctly regarded as homologous to the "primary mesoblasts" of Götte. His figures leave no doubt that these cells are the two posterior proteloblasts (*X*, *X*). His conclusions, therefore, differ from Götte's mainly in the form of statement, since he regarded the "primary mesoblasts" as forming part of the "ectoderm," while Götte regarded them as of entoblastic origin.

In my preliminary paper I first showed the true relations of the somatoblasts to the germ-layers, and v. Wistinghausen's paper (suppressed trochophore of *N. Dumerilii*), which appeared soon afterwards, contained a welcome confirmation of my general results. According to this author (whose description of the first three cleavages coincides with Götte's and my own), three sets of micromeres are separated from the macromeres, and the origin of the somatoblasts is the same as in the American species. He has, however, overlooked the left posterior micromere of the third group (d^3), the place of which, as he supposes, is taken by the second somatoblast. I am persuaded that this is an error, for two reasons; first, because I also for a long time overlooked this micromere, which is very hard to see on account of its transparency and its position, wedged in as it is beside the somatoblast; and second, because a precisely corresponding micromere is found in the embryo of the gasteropod *Crepidula* (as described by Conklin), the cleavage of which agrees with that of *Nereis*, step by step, up to the close of the spiral cleavage.[1]

Regarding the fate of the somatoblasts, v. Wistinghausen's general conclusions agree closely with my own. They differ, however, in the interpretation of the "secondary mesoblast," which v. Wistinghausen calls the "untere Urzellen des Rumpfes," and which, as he asserts, give rise to the anterior portion of the ventral ectoblasteal. The primary mesoblasts (*i.e.* after separation of the secondary mesoblast) are called "myoblasts." Since the second somatoblast contains ectoblastic as well as

[1] I have since found this micromere in four other genera of Polychæta.

mesoblastic material, he denies that the two cells arising by its fission are "primary mesoblasts," homologous with those of *Lumbricus* or *Clepsine*.

A careful examination of v. Wistinghausen's descriptions and figures has not enabled me to discover the evidence on which this conclusion is based. His figures prove simply that the "myoblasts" (*i.e.* the primary mesoblasts) sink below the surface, as I have described. There is not the slightest indication of the fate of the "untere Urzellen des Rumpfes." It appears to me that v. Wistinghausen's conclusions have been influenced more by the supposed theoretical demands of the views of Kleinenberg than by actual observation. I readily grant that my own conclusions are not yet fully established. They rest, however, on definite observations, which appear to be more complete and satisfactory than those of v. Wistinghausen.

It is difficult to take as serious v. Wistinghausen's criticism on my comparison of the "posterior teloblasts" of *Nereis* to those of the Hirudinea and Oligochæta. It resolves itself simply into this: that this comparison is inadmissible because of the lack of distinct cell-rows in the ventral plate (!). It is not necessary to waste space by replying to such a criticism.

The divergence between v. Wistinghausen's results and my own becomes more serious when the fate of the micromeres is considered; but it is clear that this is owing largely to the wide and obvious gaps in his observations. The first set of micromeres ("encephaloblasts") give rise, as he asserts, only to the cephalic lobes (Kopflappen), from which are produced the cerebral ganglia and the cephalic sense-organs. The second and third sets (the somatoblasts of course excepted) "are not concerned in the formation of the body, inasmuch as they afford no essential material for the formation of individual organs or their parts." They give rise only to "the epidermis of the annelid and an embryonic structure, namely, the præ-oral ciliated belt" (*l.c.*, p. 54). These conclusions so obviously rest upon incomplete observations that they scarcely demand examination. It is clear from v. Wistinghausen's own figures that he entirely missed the three spiral cleavages of the primary micromeres, and not one of the divisions of the other micromeres is described or figured. His statements regarding the fate of the micromeres, the origin of the prototroch, stomodæum, etc., rest

merely on sections and on general views of embryos prepared by unsuitable methods; and the errors into which he has fallen are a striking illustration of the necessity of employing a method which will give clear and definite surface-views.

2. *Comparison with Other Annelida.*

Many embryologists have made observations on the early stages of cleavage among the Polychæta, but almost without exception these stages were not brought into sufficiently definite connection with the larvæ and adult structure to admit of any detailed comparison with *Nereis*. The most complete of these studies we owe to Hatschek, whose account of *Eupomatus uncinatus* gives a clear view of the general relations of the cleavage stages to the gastrula and the larva. Even in this case, however, the history of the individual blastomeres is imperfectly known, and neither the relation of the mesoblast to the four-celled stage nor the origin of the ventral plate was determined.

I turn, therefore, to the Oligochæta and Hirudinea, the early stages of which have been far more thoroughly studied than those of the Polychæta. As a basis, I shall take Whitman's work on *Clepsine* (Nos. 27, 28) and Vejdovsky's on *Rhynchelmis* (No. 25), and my task is much simplified by the fact that Whitman has himself given a full comparison between these two forms, and between *Clepsine* and the other Hirudinea.

The eight-celled stage has the same structure, and in all probability arises in the same manner, in the three forms, the only difference being the much greater relative size of the micromeres in *Nereis*. (I agree with Whitman that Vejdovsky is probably in error in his account of the second cleavage. There is no doubt of the exact agreement of *Clepsine*, *Nereis*, and many other annelids on this point.) There is, however, a remarkable difference in the axial relations, since in both *Clepsine* and *Rhynchelmis* the large macromere marks the posterior region, as in the polyclades, and the first two cleavage-planes are inclined approximately at an angle of 45° to the median plane (see p. 454).

In *Clepsine* the large macromere first gives rise to a large cell ("neuro-nephroblast") and then divides into two "primary

mesoblasts" from which the mesoblast-bands arise. The neuro-nephroblast divides into two, four, and finally eight cells (teloblasts), from which the outer strata of the germ-bands arise. The eight teloblasts arrange themselves in two groups of four each; each of these gives rise to the germ-band of the corresponding side, which is composed of four corresponding rows of cells. Of these rows the lowermost (*i.e.* the one that ultimately lies nearest the median ventral line) gives rise to the corresponding half of the ventral nerve-cord, and is, therefore, called the neural row, the corresponding teloblast being accordingly a *neuroblast*. The adjoining two rows were believed by Whitman to be concerned in the origin of the nephridia, and were hence termed nephric rows, their teloblasts *nephroblasts*. The fourth, whose history is doubtful, is the outer row, produced by the outer or lateral teloblasts. Inside these four rows is the mesoblast-band, the whole structure constituting the "germ-band." The structure and origin of the germ-band, as thus described, has been fully confirmed in the case of *Clepsine*, and I have found an almost precisely similar structure in the germ-bands of *Lumbricus* (No. 29). Bergh (No. 1) has confirmed both Whitman's account and my own, but asserts that the "nephroblasts" and lateral teloblasts give rise to the circular muscles, and hence are to be regarded as *myoblasts*.

In *Lumbricus*, unfortunately, the origin of the neuro-nephroblasts in the cleavage has not yet been determined. In *Rhynchelmis*, however, Vejdovsky describes the origin of a group of cells that, as Whitman points out, are almost certainly to be identified with them, although Vejdovsky did not determine their later history. Of these cells there are at first two ("first and second mesomeres") successively budded forth from the large macromere. This is followed by the separation from the same macromere of a "third mesomere," which divides longitudinally to form the two primary mesoblasts. The remainder of the large macromere enters into the formation of the mesenteron, as in *Nereis*. The first and second mesomeres divide so as to form *four* large cells lying in the ectoblast at the posterior extremity of the incipient germ-bands, and there is scarcely room to doubt that these four cells represent the four posterior teloblasts of *Nereis* and the eight (at one time four) of *Clepsine* and *Lumbricus*.

Now there can be no question that the ectoblastic portion of the germ-bands in *Lumbricus* and *Rhynchelmis* is the homologue, on the one hand, of the corresponding portion in the Hirudinea, and on the other hand, of that structure in the Polychæta that I have called the ventral plate. In the Hirudinea and Oligochæta this structure is from the beginning separated into two halves, which subsequently grow together along the median ventral line. In the Polychæta the two halves are always distinguishable, but sometimes (as in *Lopadorhynchus* or in *Polygordius*) they develop in their definitive position side by side; sometimes (as in *Nereis*) they are primarily in contact, but secondarily separate and again come together along the median ventral line, as in the Oligochæta.

It follows that *the first somatoblast of Nereis is the homologue of the primary neuro-nephroblast of Clepsine*, with which it precisely agrees both in mode of origin and in ultimate fate. It differs only in the fact that it gives rise on each side to two instead of four teloblasts. In *Rhynchelmis* it is represented by the first and second "mesomeres" taken together, and it would be interesting to determine whether these two are already differentiated from one another (*e.g.* one a neuroblast, the other a nephroblast or myoblast). In *Nereis* I have been unable to distinguish between the products of the inner and outer pairs of the four teloblasts; this may, however, be owing simply to the fact that the cell-rows become indistinguishably fused together.

It is clear without further discussion that *the second somatoblast of Nereis is the homologue of the "third mesomere" of Rhynchelmis and of the primary mesoblast of Clepsine before its division into two.*

Further than this I shall not carry the comparison. It has, I think, been shown that representatives of the three leading groups of annelids show an extraordinarily precise correspondence in the cleavage of the ovum, the origin of the germ-layers, and the differentiation of the principal elements of the germ-bands; and this correspondence warrants the confident expectation that the apparently aberrant mode of development represented by *Lopadorhynchus* will be found to conform to the ordinary type when a detailed study of the early stages shall have been made.

3. *General Comparisons with Other Animals.*

It is not my purpose to undertake an extended comparison of the cleavage with that of other animals, but there are certain resemblances so striking in themselves, and so interesting when carefully analyzed, that it is impossible to pass them by. These resemblances relate especially to the cleavage of the molluscan and the polyclade ovum, and they are of such importance that I give a number of diagrams to set them clearly forth. For the sake of condensation I shall pass by most of the earlier literature and select as types the development of the Polyclade, *Discocœlis,* as described by Lang (No. 15), of the gasteropod *Neritina* (Blochmann, No. 2), and of the gasteropod *Crepidula* (Conklin, No. 4).[1]

Up to a late stage in the spiral period (twenty-eight cells) every individual blastomere and every cell-division is represented by a corresponding blastomere and a corresponding cell-division in the embryo of the polyclade, and in that of the gasteropod. In all three the first two cleavages and the upper and lower cross-furrows have the same relations. In all, three groups of four micromeres each are successively separated from the macromeres, — the first group in a right-handed spiral, the second in a left-handed spiral, and the third in a right-handed spiral, like the first. The micromeres of the second and third groups alternate with one another so as to form an outer belt of eight cells that surrounds the four primary micromeres (Diagram VII, *A*, *B*).

In all, the primary or central micromeres likewise undergo three spiral cleavages, the first right-handed, the second left-

[1] I much regret that I cannot make full use of Conklin's beautiful studies of the gasteropod cleavage, since they have not yet been published in full. The work has been carried on at Wood's Holl at the same time with my own studies on *Nereis;* and to Professor Conklin's courtesy I owe the opportunity to examine his entire set of unpublished drawings, and to verify their accuracy in respect to some of the most important stages by the study of the original preparations. This is by far the most accurate and complete study of the molluscan cleavage that has thus far been made. The resemblance to the *Nereis* cleavage is so close and extends over so long a period as to be most extraordinary. Since, however, the figures may not be published for some time, I am compelled for the present to take Blochmann's *Neritina* as my principal basis of comparison. I may add that, in the course of the past summer, Conklin has ascertained that the first cleavage-plane in *Crepidula* is not longitudinal, as he at first described it, but transverse, precisely as in *Nereis.* The preparations he has shown me seem to leave no room for doubt on this point.

handed, and the third right-handed again. The first two sets of cells thus produced alternate with each other, and thus form a second or inner belt of eight cells (*C*, *D*. *E*), interposed between

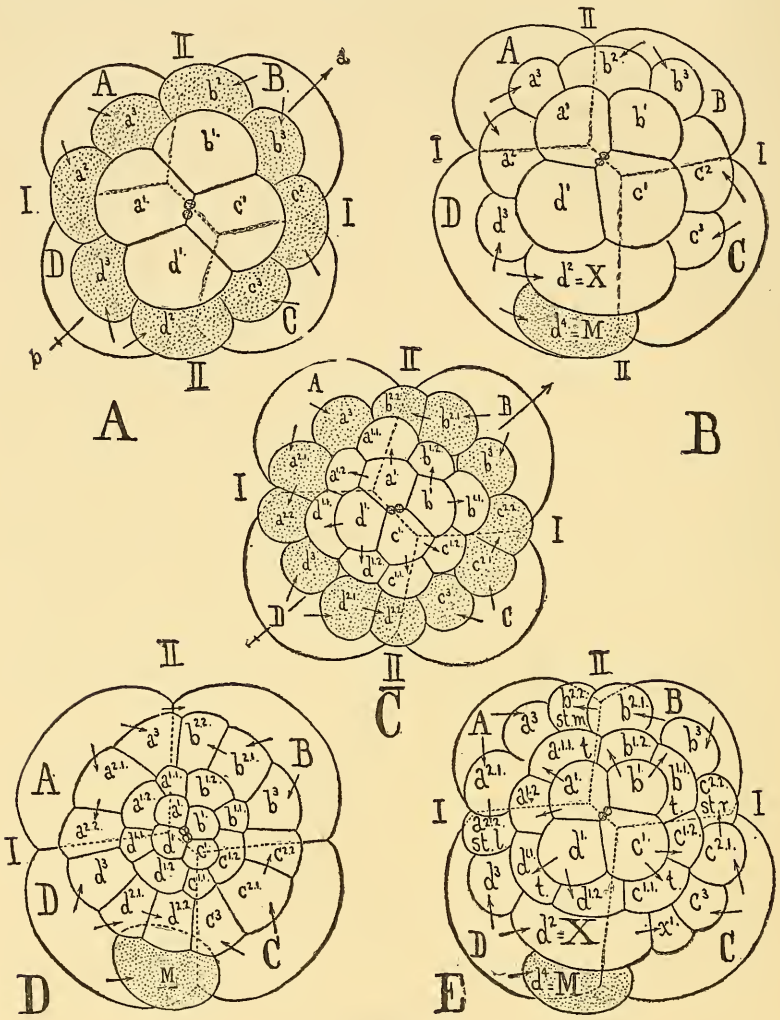


DIAGRAM VII.

A. Diagram of the polyclade embryo, showing the relations of the micromeres to the macromeres. Mesoblast shaded. The Roman numerals designate the cleavage-plans.

B. Corresponding diagram of the *Nereis* embryo.

C. Twenty-eight-celled stage of polyclade.

D. Molluscan embryo after the differentiation of the germ-layers.

E. Corresponding diagram of *Nereis*.

the central (primary) micromeres and the outer belt. Finally, the second set of micromeres divide meridionally, and in *Nereis* and *Crepidula* this can be distinctly recognized as a left-handed spiral. Thus arise four pairs of cells, with which alternate the four micromeres of the third set; and the outer belt now consists of twelve cells, which form the lips of the blastopore (*C*, *D*, *E*).

All three agree, furthermore, in the meridional division of the first-formed progeny of the primary micromeres ($a^{1.1}$, $b^{1.1}$, $c^{1.1}$, $d^{1.1}$), so that the inner belt is likewise composed of twelve cells. The third spiral cleavage of the primary micromeres gives rise to four apical cells (the "rosette-cells" of *Nereis*, the "Scheitelzellen" of *Eurylepta* and *Discocœlis*), which strikingly recall the four apical cells of the *Echinus* embryo (Selenke, No. 23). At this point the polyclade diverges from the annelid and mollusk. In the former, the differentiation of the germ-layers is complete. In the latter two, one further step is taken, by the separation of the primary mesoblast-cell from the left posterior macromere.

The general later history of the blastomeres thus formed is as follows: *In the polyclade the first group of micromeres gives rise to the entire ectoblast, the second and third groups to the mesoblast, the macromeres to the entoblast. In the mollusk and annelid, on the other hand, the second and third groups of micromeres give rise to ectoblast, like the first set, and the mesoblast arises subsequently.* This remarkable divergence between the polyclade on the one hand and the mollusk and annelid on the other is a fact of capital importance, for it proves that cells having precisely the same origin in the cleavage, occupying the same position in the embryo, and placed under the same mechanical conditions, may nevertheless differ fundamentally in morphological significance. We cannot escape the conclusion that the cell possesses a definite hereditary tendency upon which primarily its nature depends, however much its outward form or mode of division may be affected by the mechanical conditions of its environment in the body; and full weight must be given to this heredity in every attempt to interpret the origin and meaning of cleavage-forms.

Let us now pursue the comparison between the annelid and the mollusk. Blochmann describes and figures on the upper hemisphere of the *Neritina* embryo a perfectly symmetrical cross

of cells, which Conklin has also found in *Crepidula*. The arms of the cross meet at a right angle, in the centre of the upper hemisphere, and lie directly above the four respective macromeres, as in *Nereis* — *i.e.* they are inclined at an angle of 45° to the first two cleavage-planes (see Blochmann's Fig. 53). The principal portion of each arm likewise consists primarily of three cells, precisely as in *Nereis*. The resemblance is in fact so precise that at first I had no doubt the two were perfectly homologous. An exact comparison shows, however, that *the cross-cells have a totally different origin in the two cases*. In *Nereis*, the four arms arise respectively from the four primary micromeres, after the completion of their three spiral divisions, and the remains of the four micromeres (a^1, b^1, c^1, d^1) persist as the pole-cells at the extremities of the cross. The composition of the arms is therefore, a^1, $a^{1.5}$, $a^{1.4}$; b^1, $b^{1.5}$, $b^{1.4}$, etc., the centre being occupied by the rosette-cells, $a^{1\,3}$, $b^{1.3}$, etc. (*cf.* Figs. 37, 38). In *Neritina*, on the other hand (accepting Blochmann's conclusions), the arms are derived from the *second set of micromeres*, the centre being occupied by the four primary micromeres. The arms of the cross in the two forms have in fact the following composition as compared with one another (I use throughout the nomenclature employed for *Nereis*, which differs somewhat from Blochmann's):—

Nereis	a^1,	$a^{1.5}$,	$a^{1.4}$, — b^1,	$b^{1.5}$,	$b^{1.4}$ — etc.
Neritina	$a^{2.2.1}$,	$a^{2.2.1.1}$,	$a^{2.2.1.1.1}$, — $b^{2.2.1}$,	$b^{2.2.1.1}$,	$b^{2.2.1.1.1}$ — etc.

In other words, the cross-cells of *Neritina* correspond, in mode of origin, to derivatives of the stomatoblasts and of the first somatoblast in *Nereis!*

Professor Conklin informs me that his observations on *Crepidula* do not quite agree with Blochmann's, as the outer portion of each arm arises from the second set of micromeres, the inner portion from the first group (*i.e.* from $a^{1.2}$, $b^{1\,2}$, etc.). This, however, agrees no better with *Nereis* than Blochmann's account.

It is impossible to explain the differences between the annelidan and the molluscan cross by assuming inaccuracy of observation on Blochmann's part, since the pole-cells of the lateral arms show a peculiar granulation that may be seen in the parent-cells ($a^{2.2}$, $c^{2.2}$) from which they arise. It is certain that,

although the two crosses have exactly the same structure, they have a completely different origin. Are they to be regarded as homologous or not? The different origin of the cells does not in itself necessarily give a negative answer to this question. Aside from this, however, there is good reason for believing that they are not homologous. Conklin and Blochmann agree that, in the molluscan cross, two of the arms fall ultimately in the median line, while the other two are transverse to it. The annelidan cross, on the other hand, is inclined at an angle of 45° to the median and transverse planes. They must, therefore, give rise in the two cases to different regions of the upper hemisphere. Taking this in connection with the different history of the cells, there is every reason to believe that the annelidan and the molluscan crosses are analogous, but not homologous, structures, whose origin is in some way connected with the mechanical conditions of cleavage. What these conditions are I am unable to conjecture.

We come in the last place to the relation of the molluscan velum to the annelidan prototroch. According to *Blochmann* the velum arises from the terminal cells of the lateral arms of the cross ("Ur-velarzellen") which travel forwards, give rise to a transverse series of cells on either side, and from these arise the corresponding halves of the velum. If this account be correct, the velum has a totally different origin from the annelidan prototroch (in the annelid from $a^{1.1}$, $b^{1.1}$, $c^{1.1}$, $d^{1.1}$; in the mollusk from $a^{2.2.1}$, $c^{2.2.1}$). Does this indicate that the two structures are not homologous? I do not think that this conclusion necessarily follows.

X. General Interpretation of the Cleavage.

It is impossible to reflect upon the complicated yet perfectly ordered events of the cleavage in *Nereis* without attempting to discover the nature of the causes by which their course is determined. The completeness with which the history of the individual blastomeres can be followed and their mutual relations determined, the definite periods into which the ontogeny falls, the sudden transitions from one phase of activity to another — these and many other features of the development bring to the foreground some of the most interesting and fundamental problems of cytology. The solution of many, perhaps all, of

these problems may lie far in the future. Yet an attempt to consider them may, at least, serve one useful purpose by defining more clearly their outlines; and it is possible that the embryo of *Nereis* may prove in some respects an unusually favorable object for their investigation.

What is the significance of the spiral and bilateral forms of cleavage, and where lie the causes that determine the transformation of the one into the other? What determines the form and succession of the divisions of the individual blastomeres, which, as in the case of the first somatoblast, may have so complicated and yet so definite a history? Is the blastomere, like the ovum, a self-regulating mechanism that contains within itself the causes of its own transformations, that is wound up like a clock, as it were, and must of necessity run the course predetermined in its own structure? Or are its successive phases of activity determined or guided by influences proceeding from without — by the interaction of the cell with its fellows in the cell-complex? I scarcely need to point out that this latter question bears immediately upon that most pressing of all current general questions, the relation between the somatic cells and the germ-cells; and it is a problem upon which a flood of light is being thrown by recent investigations. It must be said at the outset that the development of *Nereis* gives no certain answer to this question. It does, however, as I believe, give strong indirect evidence which is worthy of attentive consideration.

The most striking feature in the cleavage, and the one on which the entire discussion may be made to turn, is the sudden appearance of bilateral symmetry in the cleavage. The meaning of the bilateral cleavages in themselves is perfectly obvious. They are the forerunners of the bilateral arrangement of parts in the adult; and, as such, their explanation belongs to the general problem of bilateral symmetry, which need not be considered here. The all-important point is that *the bilaterality does not appear at the beginning of development.* It appears only at a comparatively late stage, and by a change so abrupt and striking as to possess an absolutely dramatic interest. I lay especial stress on this point because it is wholly opposed to the opinion, which has of late rapidly gained ground among embryologists, that (1) the bilaterality of the adult is predeter-

mined in the ovum and therefore (2) manifests itself throughout the cleavage. The first of these propositions is a barren truism, for every adult characteristic is in one sense predetermined in the ovum. The second, however, is a premature generalization, and it does not follow from the first. *In some cases*, it is true, the cleavage does show a bilaterality from the beginning; and sometimes it is marvellously perfect, as shown, for instance, by the brilliant studies of van Beneden and Julin on the ascidian cleavage (No. 24) and of Watase on that of the cephalopod (No. 26). But this is by no means invariably the case. The earlier stages of many annelids, mollusks, polyclades, and other bilateral forms are bilateral neither in structure nor in the form of cell-division. It is true that the adult bilaterality may be in a certain way foreshadowed in the spiral period (*cf.* p. 400). But the following facts are indisputable: (1) that at no time during the spiral period is it possible to pass a plane so as to divide the body into equivalent right and left halves; and (2) that the planes of cleavage throughout this period are symmetrically distributed with respect, not to the future median plane, but to the vertical axis of the ovum.

What determines the period at which the first bilateral divisions appear? To this question a very simple and obvious answer can be given which, as I believe, gives a key to the entire development. *The bilateral asymmetry of the early stages depends mainly upon the fact that the substance of the somatoblasts* (i.e. *the mesoblast and the material of the ventral plate*) *is stored in the left posterior macromere. Bilateral symmetry is established upon the reduction of this macromere* (*D*) *to the size of its fellow* (*C*) *by the separation of the somatoblasts and their transportation to the median line. Immediately upon this event follows the appearance of bilateral cleavages throughout the embryo, except in the cells which give rise to the prototroch, a purely larval organ.* In other words, the bilateral cleavages appear as soon as the embryonic material becomes equally distributed with respect to a plane, which ultimately becomes the adult plane of symmetry. Is the correspondence between these two events a mere coincidence, or do they stand in the relation of cause and effect? Under the former alternative we must suppose that the coincidence is the result of a kind of pre-established harmony, such that the cells of the upper and lower hemi-

spheres, different as their past history has been and independent of external conditions, arrive at the period of bilateral divisions practically at the same moment. When we reflect upon the history of the nuclear spindles, the diverse forms and mechanical relations of the cells, such an assumption makes, under the theory of probabilities, a demand upon our credulity which I for my part am not prepared to meet. To accept the second alternative, however, is to admit that the form of the individual cell-divisions is in some degree controlled by influences emanating from the entire cell-complex.

That such influences exist is, however, certain in view of recent researches upon embryological mechanics. Roux, in one of his justly celebrated contributions to this subject (No. 20) showed, in the first place, that if one of the first two blastomeres of the frog-embryo be killed (by puncture with a heated needle), the remaining blastomere develops into a half-blastula, followed by a half-gastrula. He succeeded also in producing three-quarter embryos by killing one of the blastomeres of the four-celled stage. From this he drew the following conclusion (*Separat-abdruck*, p. 30): "Die Entwicklung der Froschgastrula und des zunächst daraus hervorgehenden Embryo ist von der zweiten Furchung an eine Mosaikarbeit und zwar aus mindestens vier verticalen, sich selbständig entwickelnden Stücken." In the second place, however, he showed that ultimately the missing half or fourth is perfectly restored by a process of "post-generation," which begins about the time of the formation of the medullary folds. As far, therefore, as the later stages are concerned, Roux's own results contradict the mosaic hypothesis; for the normal course of events in the uninjured blastomere, or its products, is radically altered by the changes *on the other side of the embryo*.

This significant fact is rendered still more striking by the recent experiments of Driesch (No. 6) and Fiedler (No. 7) on the embryos of sea-urchins, and by those of Chabry (No. 3) on ascidians. Driesch shows, in his extremely interesting paper, that if the two primary blastomeres of the *Echinus* embryo be completely, or even partially, separated (by shaking), each blastomere may give rise to a perfect embryo of half the normal size. The cleavage of each blastomere (whether isolated or still in partial contact with its fellow) at first follows the same course

as if it formed a part of a normal embryo, giving rise to stages of two, four, eight cells, etc., which are practically identical with the corresponding *halves* of the four-, eight-, and sixteen-celled stages, etc. As in the frog, a perfect half-blastula is produced. The opening then closes, and a blastula is then formed which differs from a normal blastula only in being half the normal size. The gastrulation and later stages follow the normal course.

This result agrees essentially with Roux's, with the interesting difference that the regeneration of the missing half takes place much earlier. It proves conclusively that in the normal development each of the blastomeres is profoundly influenced by the other; that the cell is not an isolated mechanism whose mode of action is wholly predetermined in its molecular structure. It proves in fact that the form of cell-division is determined by two factors. The first factor is the inherited tendency of the cell to pursue a definite course, a tendency which we may assume exists by virtue of a corresponding molecular or protoplasmic structure (*cf.* p. 441). The second factor is the influence upon the cell of other cells in the colony. When the second factor is removed or modified, the first is correspondingly modified, and a complete readjustment takes place. I can see no logical halting-point in the application of this principle between the embryonic and the adult stages. If the experimental results be well founded, — and it is impossible to question the validity of the combined evidence, — then no cell in the embryo or in the adult is isolated, *not even the germ-cells.*

In view of these facts there seems to be very strong reason to accept the conclusion that there is a causal connection in the *Nereis* embryo between the bilateral distribution of material and the ensuing bilateral divisions. I do not mean to assert that this connection is independent of the inherited tendency of the cells. It is probable, on the contrary, that the action has produced an hereditary effect. This result, however, only extends the causal connection over a longer period, and in nowise diminishes its significance.

We pass now to a discussion of the spiral period itself, which has many interesting and significant features. The principal datum on which the entire discussion rests is the fact that *the spiral form of cleavage has no necessary relation to the homology*

of the blastomeres, and hence is without phylogenetic significance. The truth of this proposition is at once apparent upon comparing the spiral cleavage of the annelid with that of the polyclade. The form of cleavage is identical in the two, the products extremely different, as has been pointed out at p. 441. Unless, therefore, we are prepared to maintain the absurd proposition that the mesoblast of the polyclade is homologous, not with the mesoblast of the annelid, but with the ectoblast of the lower hemisphere (including, of course, the ventral plate with the ventral nerve-cord), we cannot escape the conclusion that *exact equivalence of embryological origin is not a proof of homology*, as far, at least, as the cleavage-stages are concerned. Balfour, long ago, pointed out the fact that similarities in the general form of cleavage have no necessary relation to adult relationships, but it is a very surprising fact that a resemblance so close as that between the polyclade and annelidan ovum should be without morphological meaning. This is the more surprising because the comparative study of the annelids shows that within the limits of this group adult homologies are represented by accurate cell-homologies in the cleavage-stages (p. 436). We must conclude, however, that precisely similar modes of cleavage may arise quite independently of the nature of the materials, upon which the cleavage operates.

If, then, the spiral form of cleavage has no phylogenetic meaning, and at the same time has no direct relation to the adult form (as has been sufficiently pointed out), it must be due to mechanical conditions peculiar to the earlier stages of embryonic life. Before attempting to consider the nature of these conditions, I must call attention to a fact, which has been fully and clearly set forth in a profoundly interesting paper of Rauber's (No. 19), namely, that the mechanical laws of cell-division have been far more thoroughly investigated in plants than in animals; and it is to botany that we must look for a clue to the significance of cleavage-forms among animals. I need not review *in extenso* the brilliant researches of Sachs and others in this field, since their principal results may be found in his well-known *Pflanzenphysiologie* (Vorlesung XXIV) as well as in Rauber's paper. The essential points may be thus briefly summarized. *The form of cell-division is the result and not the cause of the form of the dividing mass;* the form of the

mass is caused by its growth as a whole, and is not a resultant of the growth of the cells individually considered. This is proved in plants by many facts, of which, perhaps, the most obvious is the existence of multicellular forms, in which the characteristic form of growth is fully determined *before the mass divides into cells.* Sachs concludes that the fundamental law of cell-division is such that the cleavage-planes primarily are vertical to one another and either vertical or parallel to the surface of the dividing mass; and he shows by a masterly analysis that the cleavage-planes in growing structures of various forms conform very nearly to the theoretical mathematical demands of this law.

From an *a priori* point of view there is every reason to believe that a like relation between growth and cell-division exists in animals, although its demonstration is difficult, especially for the reason that the two processes so generally go hand in hand. As Rauber points out, however, the segmentation of the ovum is a case in which, very often at least, there is no appreciable growth or change of form throughout a long series of cell-divisions, the ovum having assumed its form and size before the beginning of cleavage.

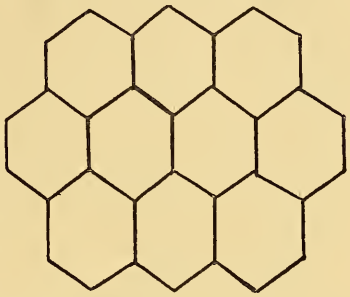
I am but expressing a commonplace of embryology in stating that the more nearly the ovum approaches its ideal form, the sphere of uniform protoplasm, the more nearly do the first three cleavages divide it into equal octants by division-planes cutting each other at right angles; in other words, the more nearly do they conform to the theoretical requirements of Sachs's law. It is interesting to find that the first three cleavages of such an ovum as that of *Amphioxus* or *Echinus* are almost exactly duplicated by the first three divisions of the spherical embryos of ferns and phanerogams. These facts in themselves create a strong presumption that plants and animals agree in the fundamental relations of growth and cell-division. If we examine the first three cleavages more narrowly we find that two types of division (apart from the bilateral) may be distinguished. The first is what may be called the true radial type (represented typically by *Amphioxus* and *Echinus*), in which the first two cleavages are perfectly vertical and the third perfectly horizontal, so that the four upper cells lie exactly above the four lower cells respectively. The second is the spiral type, represented

by *Eupomatus*, *Discocœlis*, *Nereis*, etc., in which the third cleavage is more or less inclined, so that the upper cells are displaced (apparently in all cases towards the right — *i.e.* following the hands of a watch), and in extreme cases are thus caused to alternate with the lower four.

I wish to make the point that the foregoing considerations render it probable that *the spiral type is a secondary derivative of the true radial type*, for the latter conforms more nearly to Sachs's law, and agrees with the cleavage of spherical plant-structures. Both are primarily owing to the spherical form of the ovum, but the spiral modification must be caused by some additional secondary factor. The nature of this factor seems to be very obvious, although when closely examined it is found to lead to some conclusions so important that they cannot be accepted without very strong evidence. The factor in question is *the effect of mutual pressure* among the cells. It is well known that free cells tend to assume a spherical form, whereas in masses they tend primarily to assume the same geometrical forms as soap-bubbles or other regular elastic bodies, — *i.e.* regular dodecahedrons when in bulk, regular hexagonal prisms when arranged in a single layer upon a plane surface. In the case of lifeless bodies (*e.g.* soap-bubbles) it is certain that these forms are the result of mutual pressure, and it is mathematically demonstrable that they are the forms which afford the greatest economy of space. The approximate conformity of cell-forms to these ideal mathematical forms makes it impossible to doubt that they are due to the same mechanical laws.

All these are elementary commonplaces. But the remarkable fact, and one which does not seem to be very clearly recognized, is that the effect of these mechanical conditions on the dividing cells *has become hereditary*. This I think is clearly proved by a comparison of the true radial and the spiral types of cleavage; the comparison at the same time explains a number of interesting features in the early stages, among others the cross-furrows of the four-celled stage. In the segmenting ovum we have to deal essentially with cells arranged in a single layer, either surrounding a central cavity or (as is especially clear in the *Nereis*-embryo) spread out on the spherical surface of a group of larger cells. They tend, therefore, towards the hexagonal form, though probably they never actually assume the ideal form, since they

are in a curved and not a plane layer, and differ more or less in size. Still the hexagonal form may be taken as the type without serious error. The arrangement of regular hexagons (as for instance in the honeycomb) may be roughly characterized as *alternate*, since, as shown in the accompanying diagram, the cells of each row alternate with those of the adjoining rows. Sooner or later this arrangement is assumed by the blastomeres of all segmenting ova, and the difference between the radial and the spiral types is caused simply by the earlier appearance of the alternation in the latter, as a result, undoubtedly, of different mechanical conditions. In the true radial type, beautifully shown in the cleavage of *Echinus* and *Synapta* (Selenka, No. 23), it does not appear until a late stage. In the spiral type it appears more or less distinctly from the beginning of development. This is obvious as far back as the eight-celled stage (Diagram VIII, *E*), but it is easy to show that the peculiarities of the four-celled stage are due to the same cause. The cross-furrows of this stage do not exist in the true radial type (Diagram VIII, *A*). In the spiral type they are owing to an actual or virtual displacement of the cells, so that they assume the cross-form shown in Diagram VIII, *B*, *C*, *D*, the diagonally opposing cells, *A* and *C*, lying above, and the others, *B* and *D*, below. This displacement may be characterized as a rotation, which is primarily in the vertical transverse plane, as may be seen from a comparison of Diagram VIII, *A*, *B*, *C*. In typical cases, of which *Sagitta* (Hertwig, No. 13) and *Asterina* (Ludwig, No. 16) are examples, the rotation is complete and symmetrical, the upper and lower cross-furrows being equal and at right angles to each other. Many gradations exist between this and the true radial type, one of the most interesting being the embryo of *Hydroides*, in which the two cross-furrows are equal and at right angles to one another, but so short as to escape any but the closest examination. It appears to be invariably the case that in telotethical ova, with unequal cleavage, the cross-furrows are unequal, the upper being more or less reduced, as in the embryos of many



mollusks and annelids. This reduction stands in obvious relation to the different size of the cells produced at the two poles, and requires no further discussion.

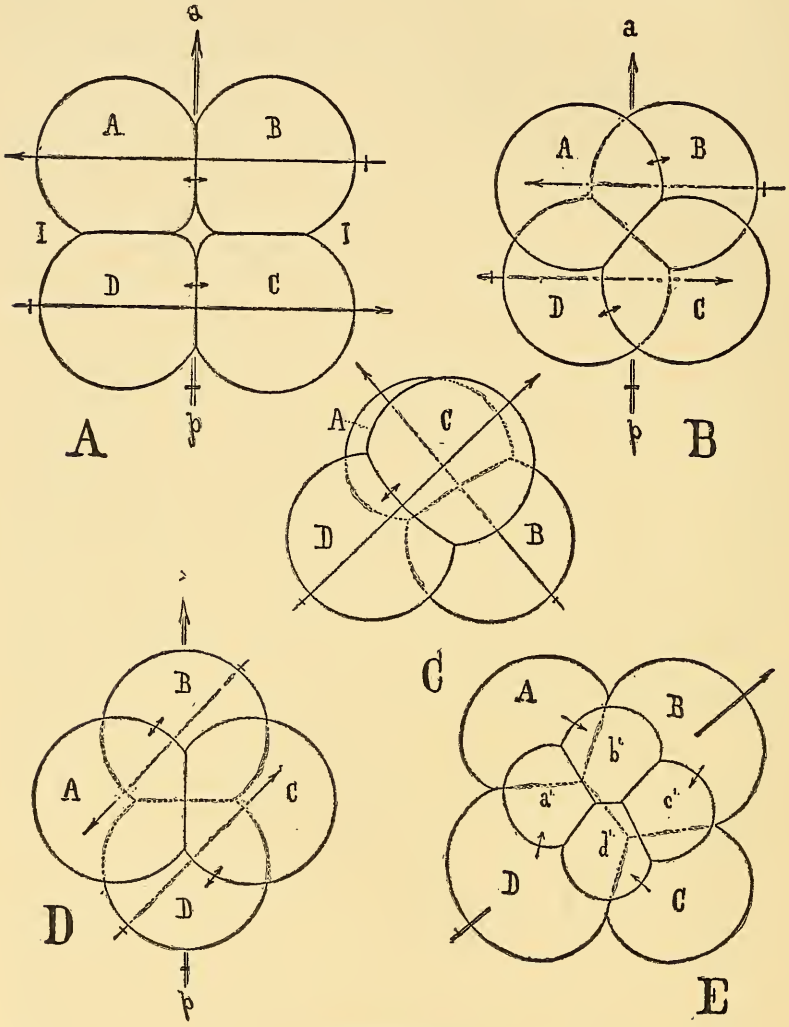


Diagram VIII.

A. Four-celled stage of true radial type (*Amphioxus, Synapta*).
B. Spiral type (*Nereis, Crepidula*).
C. Side-view of the last.
D. Spiral type (*Discocœlis*).
E. Eight-celled stage (*Discocœlis*).

We come now to the main point, which is that *the rotation of the cells is in the spiral type in many cases predetermined in the parent-cells, as is proved by the position of the spindles and by the form of division.* It is, in other words, to a greater or less extent, a virtual instead of an actual rotation. This is the case, for example, in *Asterina*, as described by Ludwig, where the division-planes of the two primary blastomeres are at right angles to each other at the second cleavage. The same is true of the polyclade embryo (Lang). It remains to be seen how far the virtual rotation is accompanied by an actual rotation of the cells after their formation. In the later cleavages of *Nereis* (*e.g.* in the formation of the rosette-cells at the fifth cleavage and of the intermediate girdle-cells at the fourth), the spindles lie in the undivided parent-blastomeres, exactly vertical to the future plane of division and the rotation is purely virtual. In the third cleavage, however, this is not the case, since the obliquity of the spindles is at first very slight and constantly increases during the division, until they form an angle of nearly 45° with the vertical axis. There is also in this case a certain amount of actual rotation after the complete separation of the cells, as may be seen by a comparison of Figs. 11 and 12. Regarding the second cleavage, the available data are very scanty, since this stage has not been accurately examined with reference to the point. I can state positively, however, that in *Ascaris megalocephala* (which, through the courtesy of Dr. Boveri, I have been enabled to study in the living state as well as in preparations) there is a very extensive actual rotation in the four-celled stage, after the full completion of the division. The value of this case as an illustration is, however, lessened by the fact that the second cleavage differs radically from the usual form.

To sum up, I conclude that the spiral form of cleavage is owing to a precocious appearance of the alternation of the cells, which, in its turn, is a result of mutual pressure. The "true radial" type differs from the spiral only in the fact that the alternation appears at a later period; in other words, the cleavage longer adheres to the primary type. The primary type owes its characteristics to the form of the ovum, in accordance with the general laws of cell-division. Thus the characteristics of the spiral period are, in their broadest outlines, the result of mechanical conditions which have no relation to the adult structure.

What, then, is the origin of bilateral forms of cleavage? It appears to me that *they must be the result of a throwing back or reflection of the adult bilaterality upon the early stages.* In some cases this influence has extended to the very beginning, as in the Cephalopod or in the ascidian, or even to the unsegmented ovum itself, as in some insects and other forms. In some cases, of which *Nereis* is a beautiful example, it has not extended so far; the early stages are still dominated by the mechanical conditions peculiar to them, and the bilateral form only appears when these conditions have been in a measure overcome.

I may call attention to the fact that there is a definite relation between the law of spiral cleavage and the fact that among annelids and mollusks it is invariably the *left* posterior macromere that is the largest. In all cases that have been accurately investigated, the first spiral cleavage of the four macromeres is right-handed, the second left-handed, and the third right-handed again. The subsequent origin of the mesoblast (as in *Nereis, Crepidula,* etc.) may be regarded as belonging to another left-handed spiral cleavage. Now the superior size of the left posterior macromere, as has been pointed out, is owing to the storage in it of the material for the somatoblasts, which, by the second and fourth left-handed spiral divisions of the macromeres, is pushed over into the middle line, where it belongs. There is, therefore, a necessary relation between the law of spiral cleavage and the storage of material in the left macromere. The exact nature of this relation, however, cannot be stated, for there is no positive evidence to show which is cause and which effect. The comparison with the polyclade, although at first sight promising, yields no result, on account of the lack of necessary data.

One other point may briefly be considered, namely, the remarkable differences in the fundamental axial relations between forms closely allied in the form of cleavage. The annelids and the mollusks show exactly parallel differences in this regard. In *Planorbis* (Rabl), *Neritina* (Blochmann), and some other gasteropods, the first two cleavage-planes are inclined at an angle of 45° to the median plane, and the representative of the "large macromere" is in the median line, precisely as in the polyclade (Diagram VIII, *D, E*). In *Crepidula,* on the other hand, the first two cleavage-planes coincide with the transverse

and median planes respectively. Among the annelids, *Nereis* agrees with *Crepidula*, while *Clepsine* (Whitman) and *Rhynchelmis* (Vejdovsky) agree with *Planorbis*, *Neritina*, and the polyclade. It is perfectly clear that this difference can have no morphological significance, but is a result of mechanical causes of some kind. Either the ectoblastic cap or the group of macromeres has been rotated 45° from its primary position, but I am at present unable to suggest an explanation that will satisfy all of the conditions of the problem. These differences certainly afford a forcible illustration of the fact that the relations of parts in the early stages of development may readily be modified by secondary conditions.

In conclusion, I may call attention to the bearing of my general interpretation of the cleavage upon the significance of the protoblasts and the study of cell-lineage. The general results show that it is necessary to be very cautious in drawing morphological conclusions from the comparative study of early cleavage-stages. I cannot entirely agree with Watase that "the earlier cleavage-processes are more fundamental, and, from the morphological standpoint, more significant than the later ones." Blastomeres having precisely the same mode of origin and precisely the same spatial relations to the rest of the embryo are by no means necessarily equivalent, either physiologically or morphologically, and the early cleavage-stages *in themselves* have little morphological value. The respective values of the blastomeres must be determined by their ultimate fate; and this is an indispensable datum for the study of comparative embryonic anatomy. *The fundamental forms of cleavage are primarily due to mechanical conditions, and are only significant morphologically in so far as they have been secondarily remodelled by processes of precocious segregation.* To this precocious segregation we must ascribe the early differentiation of the protoblasts. The facts show, however, that this process has very generally taken place in a greater or less degree; and that from the study of cell-lineage, if rightly applied, we may hope ultimately to attain a firm basis for an estimate of the different forms of gastrulas and a comparison of the germ-layers.

MUNICH, December, 1891.

APPENDIX.

Further Observations on the Cleavage and Gastrulation of Polychæta.

Since the foregoing paper was sent to press I have made at Naples an extensive series of observations on the early development of *Polymnia nebulosa*, Mont. (*Terebella Meckelii*, D. Ch.), *Spio fuliginosus*, Clp., and a form that is almost certainly the *Aricia fœtida* of Claparède. As the results cannot be published in full for some time, and are an important confirmation and extension of the work on *Nereis*, I may briefly review them here.

These three forms not only belong to three widely divergent families of Polychæta, and represent both Errantia and Sedentaria, but in addition to this differ from *Nereis* in all the conditions of embryonic development. In all three the eggs are opaque, are deposited in a jelly-mass, and in *Polymnia* and *Aricia fœtida* the trochophore is partially suppressed, the free-swimming life being of very brief duration. In all, the four macromeres continue to divide (as in *Rhynchelmis*) after the separation of the ectoblast and mesoblast; and in *Polymnia* and *Aricia fœtida* (probably also in *Spio*) there is a well-marked *embolic* gastrulation, which leads to the formation of a large blastopore.

It might, therefore, have been expected that the cleavage would differ widely from that of *Nereis*. As a matter of fact, on the contrary, it is not only quite of the same type in the three forms, but shows step by step an extraordinarily detailed and striking likeness to the *Nereis* cleavage, which may, therefore, probably be taken as typical, in all of its leading features, of an extensive series of annelids. The differences are in fact quite insignificant up to a period when the germ-layers have become fully differentiated and the somatoblasts have assumed their typical position.

I.

I will first briefly describe the facts common to the three forms and to *Nereis*, and afterwards point out some of the specific peculiarities.

The first five cleavages (to the thirty-two-celled stage) are nearly identical in all, excepting slight differences in the relative size of the blastomeres. Three sets of ectomeres are formed in the typical manner, and the somatoblasts, *X* and *M*, have essentially the same origin, position, and relation to the blastopore-margin. In all, the apical rosette and the cross arise in precisely the same manner, and at nearly the same period; and in all the first bilateral divisions first take place after the reduction of the left posterior macromere, *D*, to the size of its fellow, *C*. In all, furthermore, the primary girdle, consisting at first of eight and afterwards of twelve cells, arises exactly as in *Nereis*. The prototroch is developed in the region of the girdle-cells, but I have not yet succeeded in tracing its origin in detail. In all, finally, the first somatoblast, *X*, undergoes three unequal divisions, as in *Nereis*, thus giving rise successively to x^1 on the right side, x^2 on the left, and x^3 in the middle dorsal line. It then divides into equal parts, *X*, *X*, the posterior proteloblasts.

II.

I pass now to the leading individual peculiarities, some of which are very interesting from a comparative point of view.

(1) *Spio* differs from the others in the immense relative size of the left posterior macromere, *D*, and of the somatoblasts, *X* and *M*, derived from it.

(2) In *Spio*, *Aricia fœtida* and *Polymnia* x^1 and x^2 are very much larger than in *Nereis*, so that after their formation *X* becomes considerably reduced in size, and the posterior proteloblasts are relatively small.

(3) The later development of the cross in the same three forms differs somewhat from that of *Nereis*, the cells $c^{1.5}$, $d^{1.5}$ ("nephroblasts" in *Nereis*) being much smaller and formed in a slightly different position.

(4) *Polymnia* differs from the other forms in the fact that the second somatoblast, *M*, is from the first partially covered by the macromere, *D*, and at the time of its fission extends to the

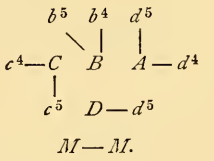
surface over only a small area. The primary mesoblasts pass into the cleavage-cavity before the formation of the blastopore; *i.e.* at a much earlier period than in the other forms, so as to approach the condition found in *Lumbricus*.

(5) In *Spio* and *Aricia fœtida* the primary mesoblasts first bud forth small superficial cells, from their anterior margin, at the posterior lip of the blastopore ("secondary mesoblast" in *Nereis*), a process which takes place at a relatively earlier period than in *Nereis; i.e.* before the fission of *X*. In *Aricia fœtida* (probably also in *Spio*) *only a single pair* of such cells are found, which are very minute and appear to be rudimentary. After their formation the mesoblasts bud forth into the cleavage-cavity (as in the "blastula" of *Lumbricus*) two rows of cells that form the mesoblast-bands.

In *Polymnia* the preliminary superficial budding seems not to take place, and the mesoblasts only divide after their complete enclosure (as in *Eupomatus*, *t.* Hatschek).

(6) In *Polymnia* and *Aricia fœtida*, (probably also in *Spio*) the macromeres undergo two additional spiral divisions after the separation of the twelve ectomeres. The first of these (fourth spiral division) is left-handed, and of the four resulting cells one ($d^4 = M$), formed somewhat earlier than the others, becomes the second somatoblast, while the other three (a^4, b^4, c^4) form part of the entoblast-plate. The second (fifth spiral division) gives rise to four entomeres (a^5, b^5, c^5, d^5), formed in a right-handed spiral, after which no further divisions take place in the entoblast-plate until after the completion of gastrulation.

The entoblast-plate now consists of eleven cells, which (in *Aricia fœtida*) assume the bilateral arrangement shown in the following diagram:—



(7) In *Polymnia* and *Aricia fœtida* (*Spio* not observed) an embolic invagination now rapidly takes place. The blastopore is at first elongated, its floor being formed (in *Aricia fœtida*) by *D*, *B*, and b^4, which lie in the median line, and its posterior limit by the primary mesoblasts, *M*, *M*. Thus (in *Aricia*

fœtida) *the first two cleavage-planes are oblique to the plane of symmetry*, as in *Clepsine* or *Rhynchelmis*, and differ from their position in *Nereis*. This difference is, however, caused simply by late displacements of the entomeres, and does not affect the earlier stages; it is, therefore, without morphological significance.

(8) The blastopore assumes a triangular form by the narrowing of its posterior portion. It appears to close completely from behind forwards, and the mouth afterwards appears at the point of final closure, *i.e.* in front.

(9) In *Aricia fœtida* the primary mesoblasts pass into the interior as the blastopore closes.

I have followed up to the thirty-two-celled stage the cleavage of a series of *Hydroides*[1] which agrees closely in development with the "Eupomatus uncinatus" studied by Hatschek and is of special interest as a representative of the so-called "equal cleavage" among annelids. The order and direction-planes of the divisions are nearly the same as in the other forms, but the spiral symmetry is complete up to the latest stage observed. The first four blastomeres, *A*, *B*, *C*, *D*, are exactly equal. At the third cleavage four slightly smaller upper cells, a^1, b^1, c^1, d^1 ("micromeres") are separated, in a right-handed spiral, from four lower "macromeres." The fourth cleavage agrees closely with that of *Polymnia*, *Nereis*, etc., but the micromeres of the second group, a^2, b^2, c^2, d^2, are of exactly equal size, and are but little smaller than the macromeres. The fifth cleavage is likewise essentially like that of the other forms, and the third set of ectomeres, a^3, b^3, c^3, d^3, are much smaller than the second set (a^2, b^2, etc.).

The embryo now (thirty-two-celled stage) agrees essentially in the arrangement of the blastomeres with the corresponding stage of the "unequal type" (*Nereis*, etc.), but differs from it (*a*) in the equal size of the four macromeres, and (*b*) in the lack of a differentiated first somatoblast (*i.e.* d^2 is no larger than a^2, b^2, c^2). It is at this period that the second somatoblast, *M*, is formed in the unequal type, where, as I have shown above (*Polymnia*, *Aricia fœtida*), it forms one of the four cells (a^4, b^4,

[1] The species is related to *Hydroides* ("*Eupomatus*") *uncinatus*, but differs from it both in the looser and more delicate growth of the tube, and in the more numerous divisions in the crown of the operculum.

etc.) produced at the fourth spiral division of the macromeres. In *Hydroides* these four cells now arise in a left-handed spiral, as in the other forms, but they are equal in size and are formed simultaneously. If the analogy holds, one of these cells (d^4) should be the equivalent of the second somatoblast, *M*, from which the mesoblast arises, the other three (a^4, b^4, c^4) forming part of the entoblast-plate. I have not yet succeeded, however, in tracing the cytogeny with certainty beyond this point, and the origin of the mesoblast therefore still remains undetermined. Should my surmise prove well founded, we would have a very simple explanation of the difference between the equal and unequal types of cleavage in annelids — a difference which has hitherto seemed to involve a difficult problem with regard to the mesoblast.

NAPLES, April, 1892.

POSTSCRIPT.

While correcting the last pages of the proofs of this paper I received Oscar Hertwig's extremely interesting work entitled "Urmund und Spina bifida," etc. [*Arch. f. Mic. Anat.*, Bd. 93, Heft III., 1892], in which the author, after a critical review of the work, especially of Roux, Driesch, and Chabry, throws the immense weight of his authority on the side of the same conclusions that I have adopted at p. 447 regarding the dependence of the development of individual blastomeres on that of the whole embryo. In opposition to Roux, Hertwig maintains that, (1) "Die Entwicklung eines Organismus ist keine Mosaikarbeit," and, (2) "die Theile eines Organismus entwickeln sich in Beziehung zu einander oder die Entwicklung eines Theiles ist abhängig von der Entwicklung des Ganzen" (p. 480).

It seems to me, however, if I may venture the suggestion, that Hertwig underestimates the importance of early differentiation among the blastomeres (*i.e.* the hereditary element in the development of individual parts), and that the mosaic view may still, *in a modified form*, be of value. In the echinoderm embryo the individual blastomeres show very little morphological differentiation until a late period. In the annelid such differentiation exists from the very beginning of the cleavage, and the mosaic appearance of the development cannot be overlooked. The facts seem to accord best with the hypothesis that the blastomeres are capable within certain limits of pursuing their individual development, yet at the same time depend *in a greater or less degree* on that of the whole. How far this dependence goes, and how far the various blastomeres may be capable of replacing one another, is a question to be determined not by analogy, but by direct experiment.

NAPLES, May 3, 1892.

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LETTERING OF THE PLATES.

The blastomeres are lettered according to the following system, for an illustration of which see Diagram, p. 378: —

A, B, C, D. The four primary blastomeres and the corresponding macromeres or entomeres.

a^1, b^1, c^1, d^1. First group of micromeres.

a^2, b^2, c^2, d^2 (X). Second group of micromeres.

a^3, b^3, c^3, d^3. Third group of micromeres.

Their products are in general lettered according to the principle illustrated in the diagram, except in the case of the somatoblasts, the four macromeres, and the four primary micromeres, which retain their original lettering throughout (*cf.* Diagram, p. 396).

$$a^2 \left\{ \begin{array}{l} a^{2,1} \left\{ \begin{array}{l} a^{2,1,1} \\ a^{2,1,2} \end{array} \right. \\ a^{2,2} \left\{ \begin{array}{l} a^{2,2,1} \\ a^{2,2,2} \end{array} \right. \end{array} \right. \text{ etc.}$$

Additional letters as follows: —

a.c. Anal cirrhi.
a.f. Anal sensory flagellum.
an. Anterior.
a.t. Apical tuft of cilia.
bp. Blastopore.
dor. Dorsal region.
e. Eye-spot.
ec. Ectoblast.
e.n. Entoblast-nuclei.
f. Cross-furrow.
f.a. Frontal antennæ.
f.b. Frontal bodies.
h.k. Head-kidney.
inf. Inferior (post-trochal) region.
i. Jaws.
l. Left side.
l.d. Latero-dorsal region.
l.m. Longitudinal muscles.
M. Second somatoblast, mesomere, primary mesoblast.
m. Secondary mesoblast.
m.b. Mesoblast-band.
mes. Mesenteron.
mh. Mouth.
ms. Mesotrochal ciliated belt.
n. Nephroblast.
n.p. Neural plate.
o.d. Oil-drop.
p. Prototrochal cell.
p.a. Pigment-area.
par. Paratroch.
p.c. Polar cell.
pig. Pigment.
p.l. Palpi.
pr. Prototroch.
p.p. Parapodia.
ps. Posterior.
p.t. Post-trochal cells.
r. Right side.
s. Setæ.
s.g. Stomodæal gland.
s.h. Sense-hairs.
s.s. Seta-sac.
st. Stomodæum.
st.l. Left stomatoblast.
st.m. Median stomatoblast.
st.r. Right stomatoblast.
sup. Upper (supra-trochal) region.
t. Trochoblast.
t.c. Tentacular cirrhi.
v. Ventral.
v.p. Ventral plate.
X. First somatoblast, and the resulting teloblasts.
x. Derivatives of *X.*
z. Zona radiata.

EXPLANATION OF PLATES.

All of the figures, unless otherwise stated, were drawn with the aid of the camera, but in many cases the finer details have been added free-hand to the camera sketch. Most of the figures were drawn from a single specimen, but in a few cases, in order to economize space, a single figure combines the sketches from more than one specimen. In the later stages, for the most part, no attempt has been made to reproduce the texture of the protoplasm, but it is of such glass-like transparency that it is fairly well represented by the shading of the figures. The coloring of the figures was an afterthought, and was adopted for purely practical reasons. Although the effect of the drawings is injured by it, so much is gained in clearness and facility of comparison that I feel sure of the approval of every reader who has labored through with a long series of imperfectly described plates.

All of the figures, unless otherwise stated, are from *N. limbata*, Ehlers. The enlargement is in most cases about 400 diameters.

PLATE XIII.

[Figs. 1 to 6, 7*a*, and 10 from living specimens; the others from preparations.]

FIG. 1. Unsegmented egg, from the upper pole, before the extrusion of the polar cells. Zona radiata still present.

FIG. 2. Side-view after the formation of the polar cells and disappearance of the zona.

FIG. 2*a* to 2*d*. Four stages in the first cleavage; 2*a* and 2*b* are side-views of successive stages of the same egg; 2*c* is from the upper pole in the earlier part of the division, and 2*d* from the lower pole at a later stage, showing the still undivided bridge of protoplasm on the lower side.

FIG. 3. Completed two-celled stage from the upper pole; *AB* the anterior, *CD* the posterior blastomere (1 h. 55 m.).

FIG. 4. The same egg from the upper pole; second cleavage in progress; the anterior blastomere divided into *A* and *B*, the posterior incompletely divided (2 h. 10 m.).

FIG. 4*a*. View from the lower pole of slightly later stage, showing the cross-furrow *f*, although *CD* is still incompletely divided (2 h.).

FIG. 5. Four-celled stage from the upper pole. The fainter lines represent the cleavage-lines of the lower pole, seen through the transparent vitellus. The deutoplasm-spheres omitted (2 h. 19 m.).

FIG. 6. Four-celled stage, from the right side.

FIG. 7. View from the upper pole of an egg (preparation) about to divide into eight cells, showing the position of the spindles. The stars represent the upper asters; the small circles, the centres of the lower asters.

FIG. 7*a*. Side-view of third cleavage (2 h. 20 m.).

FIG. 8. View from the upper pole of an egg later in the third cleavage, to show the position of the spindles.

FIG. 9. Side-view of the last.

FIG. 10. Side-view of completed eight-celled stage.

PLATE XIV.

[Figs. 11–17, 20 from life; 18, 19, 21, 22 from preparations.]

FIG. 11. The same egg shown in Figs. 3, 4, 5, immediately after completion of the third cleavage (2 h. 33 m.).

FIG. 12. The same seven minutes later.

FIG. 13. Fourth cleavage, from the upper pole (3 h. 21 m.).

FIG. 14. The same egg; end of the fourth cleavage (3 h. 30 m.).

FIG. 15. Fourth cleavage; posterior view, showing origin of the first somatoblast (*N. megalops*).

FIG. 16. Fourth cleavage, from the right side (2 h. 40 m.).

FIG. 17. The same egg, nearly in the same position, in the sixteen-celled stage (2 h. 55 m.).

FIG. 18. Optical longitudinal section of sixteen-celled stage.

FIG. 19. Beginning of the fifth cleavage, from the upper pole; primary micromeres preparing for their second spiral division (*cf.* Fig. 14).

FIG. 20. Twenty-two-celled stage, immediately following the last, from the upper pole. First division of *X*, formation of the two posterior tertiary micromeres c^3, d^3 (3 h. 58 m.).

FIG. 21. Rear view of same stage. Division of *X*, spindles of c^3, d^3.

FIG. 22. The same embryo, from the left side.

PLATE XV.

[Figs. 23, 28, 29, 32 from life; the others from preparations.]

FIG. 23. Twenty-nine-celled stage, from upper pole. The trochoblasts have divided radially (completing twelve-celled girdle); the four tertiary micromeres formed, secondary micromeres still undivided (3 h. 43 m.).

FIG. 24. Succeeding stage, from right side. Second group of micromeres in division.

FIG. 25. Thirty-two- (four-) celled stage, right side-view. Third spiral cleavage of a^1, b^1, c^1, d^1 in progress ($4\frac{1}{2}$ h.).

FIG. 26. Anterior view of the same embryo.

FIG. 27. From the upper pole. Third spiral cleavage of a^1, b^1, c^1, d^1 (formation of apical rosette). Transition from thirty-two- to thirty-six- celled stage.

FIG. 28. Thirty-six-celled stage, from the upper pole (4 h. 7 m.).

FIG. 29. Thirty-eight-celled stage, rear view. Second division of X. Origin of second somatoblast (4 h. 55 m.).

FIG. 30. Stage immediately following the last. First stage of transitional period. The two posterior primary micromeres, c^1, d^1, preparing for their first bilateral division (5 h. 15 m.).

FIG. 31. Forty-celled stage. Third (median dorsal) division of X. Bilateral division of c^1, d^1 completed (forming $c^{1\cdot4}$, $d^{1\cdot4}$) (6 h. 30 m.).

FIG. 32. Forty-three- (typically forty-two-) celled stage. Posterior view of a living specimen followed from a stage precisely like Fig. 29. Third division of X completed, interruption of the girdle by the displacement of $d^{1\cdot2}$. Fission of the second somatoblast to form the primary mesoblasts, $M.M.$ (5 h. 25 m.).

FIG. 33. Left side-view of peculiar thirty-celled stage in which the apical rosette is not yet present, though the second somatoblast is formed. Second group of micromeres just dividing. Second division of X not yet effected (7 h.).

FIG. 34. Optical longitudinal section, thirty-eight-celled stage; position of the left stomatoblast ($a^{2\cdot2}$) indicated by the dotted line.

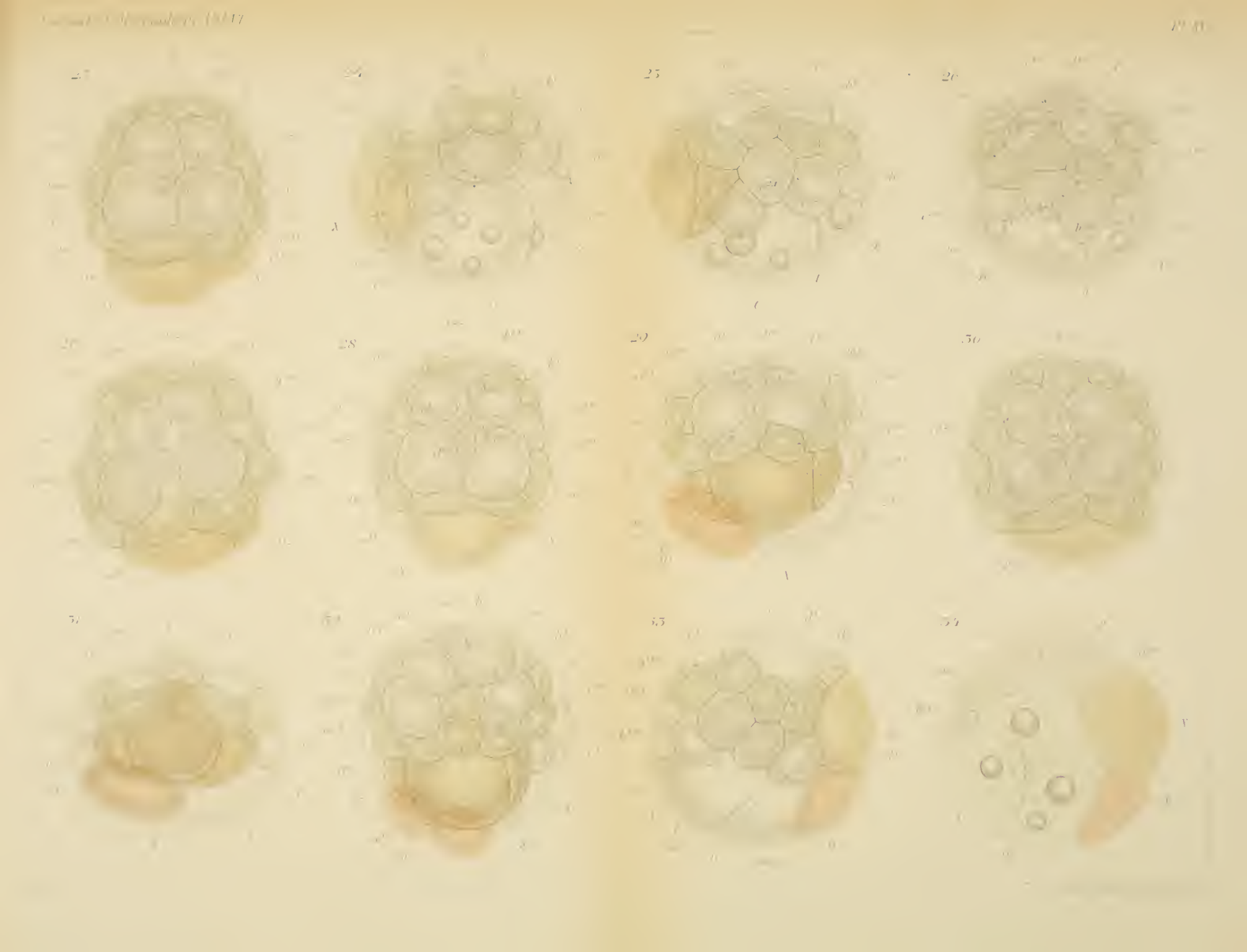

PLATE XVI.

[All of the figures from preparations.]

FIG. 35. Transition from forty-two- to fifty-eight- celled stage. View from the upper pole, showing first bilateral division of a^1, b^1, establishment of the cross, transformation of the girdle into the prototroch (5 h. 30 m.).

FIG. 36. Anterior view of the same specimen.

FIG. 37. Posterior view, about fifty-eight cells. Second bilateral division of c^1, d^1 to form the nephroblasts, $c^{1.5}$, $d^{1.5}$. Spindle of fourth division (fission) of X (5 h. 30 m.).

FIG. 38. Complete establishment of bilaterality. Immediately following the last. Formation of the nephroblasts and fission of X completed. Delayed division of $c^{1.2}$ (5 h. 30 m.).

FIG. 39. Second bilateral division of a^1, b^1, forming $a^{1.5}$, $b^{1.5}$. Division of $c^{1.4}$, $d^{1.4}$. Beginning of the enclosure of the nephroblasts (6 h. 30 m.).

FIG. 40. Third bilateral division of c^1, d^1 to form $c^{1.6}$, $d^{1.6}$; division of $a^{1.4}$, $b^{1.4}$ (7 h.).

FIG. 41. Third bilateral division of a^1, b^1 to form $a^{1.6}$, $b^{1.6}$; division of $a^{1.5}$, $b^{1.5}$. The nephroblasts nearly enclosed.

FIG. 42. Fourth bilateral division of c^1, d^1 to form $c^{1.7}$, $d^{1.7}$; fifth division of X (7 h. 30 m.)

FIG. 43. Posterior view of the same.

FIG. 44. Right side-view, somewhat from above, after the fourth bilateral division of c^1, d^1. At the left upper side the nephroblast is shown in optical section, below $d^{1.6}$ (7 h. 30 m.).

FIG. 45. Right side-view after enclosure of the nephroblast and the beginning of its migration. Fifth bilateral division of c^1, d^1. The proteloblasts (XX) have divided (eighth division of X) to form the four posterior teloblasts (X, X, X, X) (8 h. 30 m.).

FIG. 46. Rear view of slightly earlier stage (8 h. 30 m.).

PLATE XVII.

[All of the figures from preparations.]

FIG. 47. Postero-ventral view, thirty-six-celled stage. Origin of the second somatoblast (6 h. 15 m.).

FIG. 48. Succeeding stage, thirty-eight cells (*cf.* Fig. 30) (5 h. 15 m.).

FIG. 49. Postero-ventral view. Fission of the second somatoblast to form the primary mesoblasts. Transition from Figs. 31 to 32 (6 h. 15 m.).

FIG. 50. Rear view of same stage as Fig. 37. Fission of *X* (fourth division), division of d^3, c^3, x^2; second bilateral division of c^1, d^1 (6 h. 15 m.).

FIG. 51. Ventral view immediately after the fission of *X* (*cf.* Fig. 38) (7 h.).

FIG. 52. Rear view. Fifth division of *X*, x^1 dividing, x^2 divided into two (6 h.).

FIG. 53. The same stage, seen more from the ventral side; x^2 undivided, x^1 dividing. Fifth division of *X*. First gemmation of primary mesoblasts (6 h.).

FIG. 54. Postero-ventral view. Sixth division of *X* (*cf.* Figs. 42, 43) (7 h. 30 m.).

FIG. 55. Ventral view of later stage. Four secondary mesoblast cells have been formed, the primary mesoblasts are nearly covered in, and the blastopore is nearly closed (9 h.).

FIG. 56. Slightly later stage. Eighth division of *X* (fission of the proteloblasts), gemmation of the primary mesoblasts (probably the third), approximation of the stomatoblasts, division of d^3 (*cf.* Figs. 45, 46) (9 h. 45 m.).

FIG. 57. Similar view of later stage (the same specimen shown in Fig. 74) (9 h. 30 m.).

FIG. 58. Rear view of still later stage, showing the four posterior teloblasts (8 h. 30 m.).

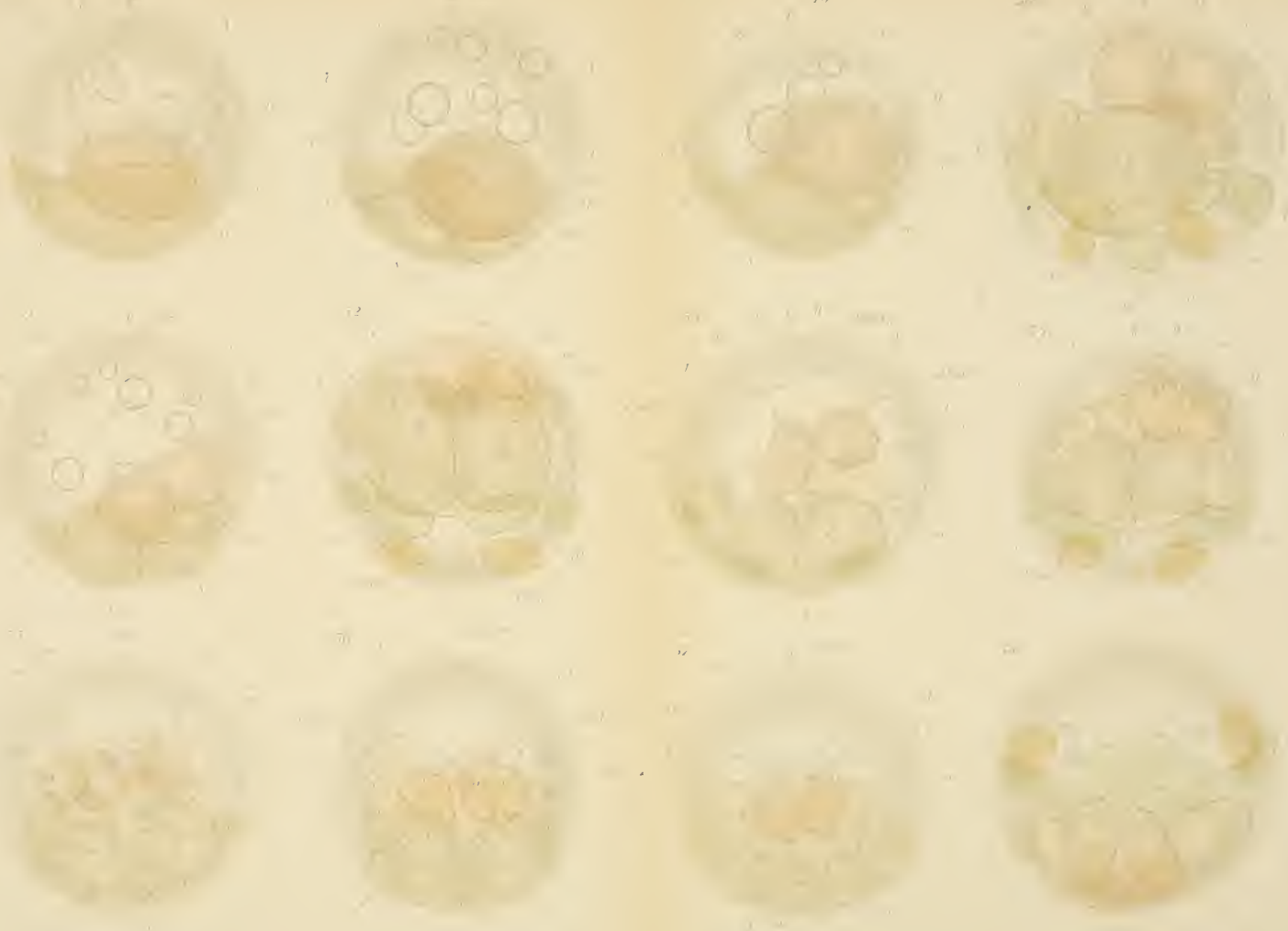

PLATE XVIII.

[All excepting Fig. 60 from preparations.]

FIG. 59. Rear view of first ciliated stage. Ninth division of X (13 h.).

FIG. 60. Living embryo in the same stage (10 h.).

FIG. 61. Postero-ventral view, after completion of the tenth division of X (11 h.).

FIG. 62. Ventral view of nearly the same stage, showing the relations of the stomatoblasts, blastopore, mesoblasts, head-kidneys, prototroch, and the posterior teloblasts (13 h.).

FIG. 63. Similar view of later stage, after the eleventh division of X (disappearance of the outer teloblasts), and closure of the blastopore. Extension of the head-kidneys, infolding of the blastopore-region, convergence of the stomatoblasts (13 h.).

FIG. 64. Rear view of nearly the same stage (11 h. 30 m.).

FIG. 65. Succeeding stage, showing division, displacement, and initial separation of the residual teloblasts (twelfth division of X).

FIG. 66. Slightly later stage with symmetrical division of the products of the outer teloblasts (11 h. 30 m.).

FIG. 67. Similar view of still later stage. Separation of the residual teloblasts, appearance of the rudimentary dorsal region, extension of the head-kidneys (14 h.).

FIG. 68. Rear view of still later stage (14 h.).

FIG. 69. Similar view of later stage (18 h.).

FIG. 70. Postero-ventral view of the latest stage in which the residual teloblasts can be distinguished. The upper part of the figure in surface-view (prototroch, residual teloblasts), the lower part in optical section (entoblast, mesoblast, ventral plate, pigment-plug) (14 h. 30 m.).

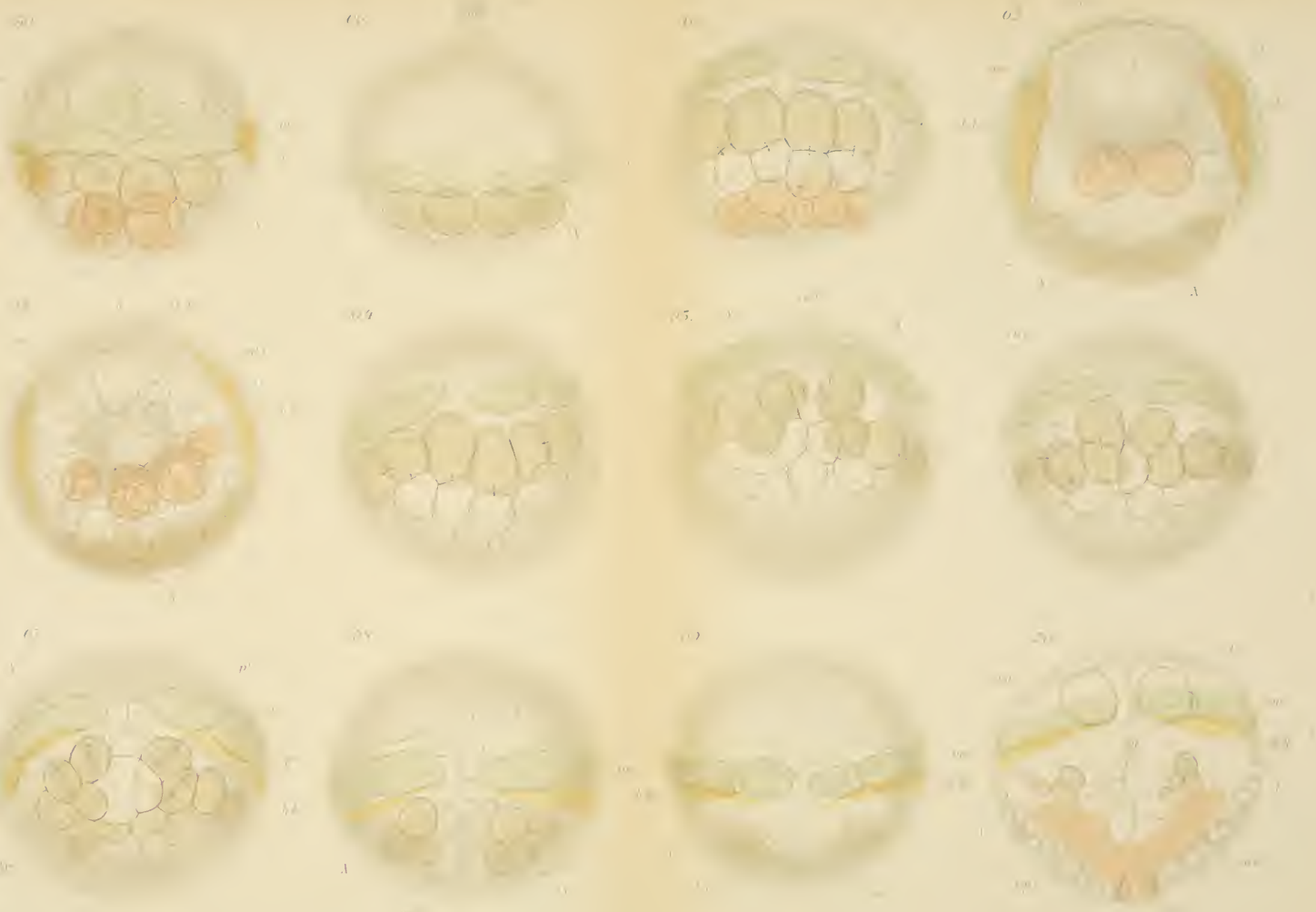

PLATE XIX.

[All of the figures from preparations.]

FIG. 71. Longitudinal optical section about the time the blastopore closes. Position of the prototroch indicated by the faint lines (9 h. 45 m.).

FIG. 72. Similar view after the first gemmation of the primary mesoblasts (the same specimen shown in Fig. 41) (7 h. 30 m.).

FIG. 73. Slightly later stage, showing gemmation of one of the mesoblasts. The section is somewhat oblique and shows the hinder part of the other mesoblast wedged in between the dividing cell and the posterior teloblast (8 h. 30 m.).

FIG. 74. Right view of the same specimen shown in Fig. 57. Nephroblast passing beneath the prototroch. Derivatives of c^1 in division (9 h. 30 m.).

FIG. 75. Later stage in similar view. Head-kidney extending itself beneath the post-trochal cells (offspring of c^2) (12 h. 30 m.).

FIG. 76. Similar view of the same embryo shown in Fig. 66. Extension and canalization of the head-kidney (11 h. 30 m.).

FIG. 77. Left side-view of about the same stage shown in Fig. 67. The head-kidneys nearly surround the body, the prototroch is double; prostomial depression still present; first appearance of the pigment (14 h.).

FIG. 78. Left side-view of same stage as Fig. 68. Prototrochal region in surface-view (also the left residual teloblast), the remainder in optical section (*cf.* Fig. 88). Formation of the pigment-area; its relations to the stomatoblasts (13 h. 30 m.).

FIG. 79. Ventral view of the same stage. The position of the residual teloblasts indicated in optical section (15 h. 45 m.).

FIG. 80. Similar view of later stage. Stomodæal arc, pigment-area, mesoblast-bands (18 h.).

FIG. 81. Completion of the stomodæum, demarcation of the pigment-plug, position of the mesoblast-bands. Last traces of the residual teloblasts (?) (20 h.).

FIG. 82. Left side-view of the same specimen. Prototroch, eye-spot, and frontal bodies in surface-view. The stomodæum and pigment-area in juxtaposition (20 h.).

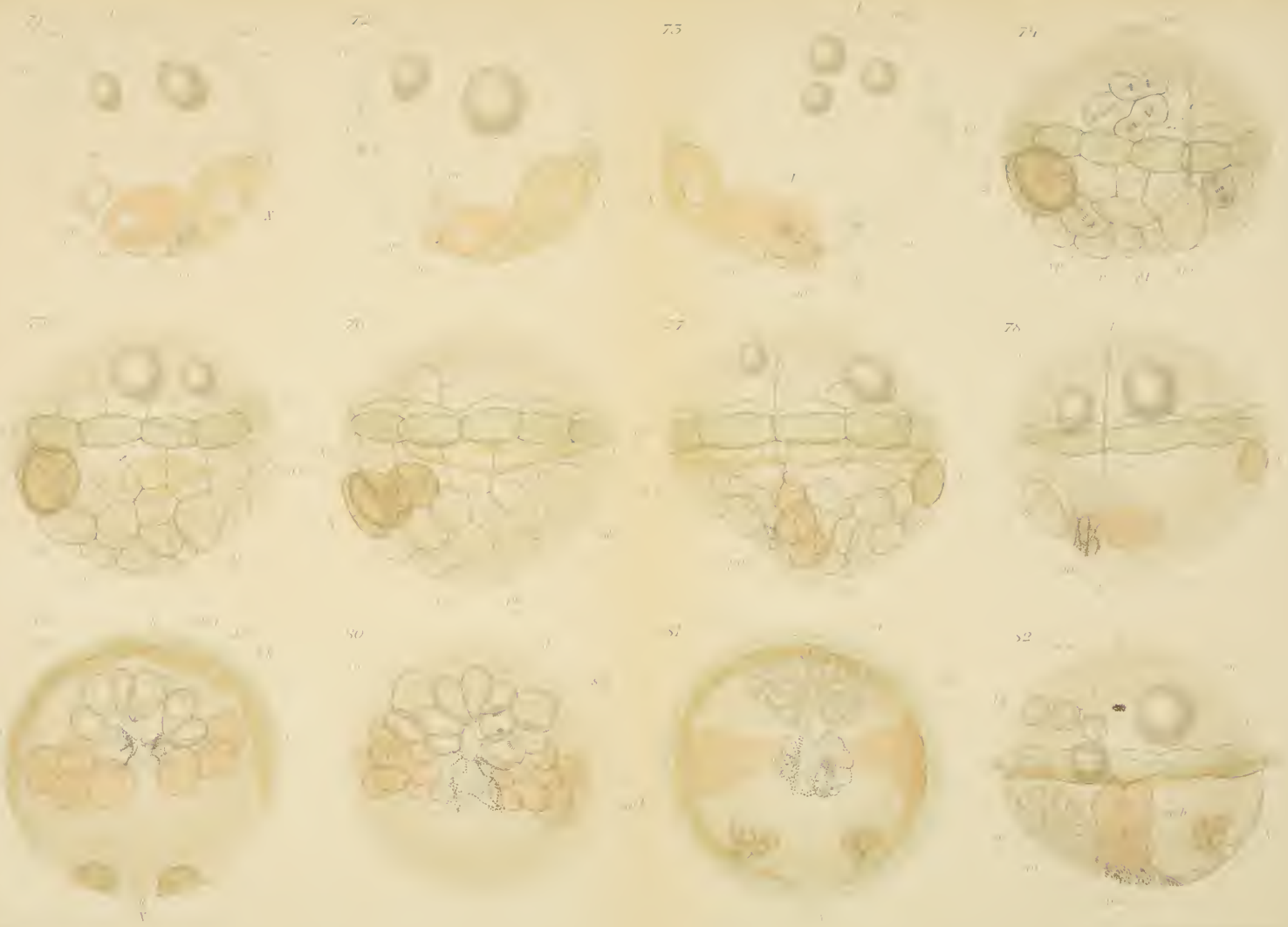

PLATE XX.

[All of the figures from preparations. Prototrochal pigment, and the cilia, from living specimens.]

FIG. 83. Ventral view. Ingrowth and concrescence of the neural plates, separation of the stomodæum and pigment-area; first appearance of metamerism (24 h.).

FIG. 84. Right side-view of the same specimen (slightly distorted by pressure).

FIG. 85. Later stage, right side-view. Formation of the setæ, longitudinal muscles, parapodial cirrhi (40 h.).

FIG. 86. The same specimen from the upper pole. First and second cleavage-lines, cross-furrow, eye-spots, frontal bodies. *Cf.* the cleavage-stages.

FIG. 87. The same specimen, ventral view. Concrescence of the neural plates, growth of the ventral region, overlapping of the head-kidneys (40 h.).

FIG. 88. Actual longitudinal section of a stage like Fig. 78. Relations of the ventral plate, stomodæal cells, primary mesoblasts, entoblast-nuclei, and the inward migrating cells of the pigment-area with their pigment (14 h.).

FIG. 89. Oral view of early stage in the elongation. Protrusion of the setæ (43 h.).

FIG. 90. Protrusion of the parapodial cirrhi. Apical and anal sense organs, *migration of the pigment-cells* (60 h.).

FIG. 91. Typical three-segmented larva, dorsal view. Completed migration of the pigment-cells, appearance of the mesotrochal ciliated belts, circular muscles, three pairs of eye-spots, first pair of tentacular cirrhi (post-trochal), and anal cirrhi (60 h.).

FIG. 92. Head of later stage (4½ d.) in ventral view. Demarcation of the head, appearance of the jaws, growth of the frontal antennæ, tentacular cirrhi, palpi, etc. Interruption of the prototroch.

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ON

THE PHENOMENA OF SEX-DIFFERENTIATION.

S. WATASÉ.

In the fifty-seventh Exercitation of his work *On Animal Generation*,[1] Harvey states that he has frequently wondered how it happens that the offspring, mixed as it is in so many particulars of its structure and constitution, and with the stamp of both parents so obviously upon it in many parts, should still escape all mixture in the matter of sex, and that it should uniformly prove either male or female.

An obvious inference that suggests itself from this point of looking at the problem, as stated by Harvey, is that we may here be dealing with two questions which are independent of each other, viz.:

(a) *The phenomena of heredity, or the mixture of the parental characteristics in the offspring;* (b) *The phenomena of sexual differentiation in the organism, in which the parental characters have already been mixed.*

Without therefore weakening even in the least degree the singularly suggestive form in which Harvey's reflection is put, we may for the sake of convenience separate the first half of the paradox from the second and consider them separately as two independent problems. We are, however, concerned at present with the second portion of the problem only, or the phenomena of sexual differentiation of the young developing organism in which the materials representing two parental characters already exist. It does not make any difference from our point of view whether this mixture of parental characters has taken place *directly*, in which case the embryo is the immediate outcome of the sexually fertilized ovum, or *indirectly*, in which case such mixture may have taken place some generations back, as

[1] *On Animal Generation*, 1651, London. The works of William Harvey, Willis' edition, 1847, p. 429.

must be considered to be the case in those eggs which are produced parthenogenetically.

The present paper is the preliminary statement of my conclusions on this subject, as based principally on my studies in the line of work recently inaugurated by Auerbach,[1] who investigated the sexual substance of male and female organisms by means of differential staining. Auerbach's method has been applied with a certain modification, in two special lines of study, viz. the phenomena of spermatogenesis and of fecundation. This afforded me the opportunity of tracing the micro-chemical reaction of the male sexual cell through all stages of its transformations from the moment of its origin in the seminiferous gland of the paternal organism, until it ends in the formation of a mature male pronucleus ready to unite with the female pronucleus. The principal point which led to the writing of the present paper consists in the fact that *the micro-chemical reaction of the sperm-nucleus, which is entirely different from that of the ovum-nucleus during the earlier stages of its existence, becomes essentially like that of the female pronucleus at the moment of fecundation.* Thus the distinction of sexes in the nuclei of the germ-cells, which Auerbach has so clearly demonstrated with specific stains in a number of cases, disappears completely at the close of fecundation, so far as such a point can be determined by the micro-chemical test.[2] The full bearing of this fact upon the subject of our discussion, as well as the similar observation of Lukjanow,[3] I shall attempt to point out later.

As has been truly said, the distinction of sex is probably the most nearly universal single attribute or property of organized beings. According to one view, the difference of sex is the absolute difference of material which enters into the formation of the male and the female organism. There is also

[1] L. Auerbach, *Zur Characteristik von Ei und Samen*, Berl. Klin. Wochenschr., 1891, xxviii, 908; *Über einen sexuellen Gegensatz in der Chromatophilie der Keimsubstanzen, nebst Bemerkungen zum Bau der Eier und Ovarien niederer Wirbelthiere*, Sitzungsber. der K. Preuss. Akad. d. Wiss. zu Berlin. XXXV, Heft VII, 1891.

[2] Some facts bearing on this subject may be found in the two following abstracts of mine, *The Origin of the Sertoli's Cell*, American Naturalist, May, 1892; *On the Significance of Spermatogenesis*, American Naturalist, July, 1892.

[3] Lukjanow, *Einige Bemerkungen über sexuelle Elemente beim Spulwurme des Hundes*, Arch. f. Mikr. Anat., Vol. 34, 1889.

a view in which the maleness and the femaleness of the organism may be described as due to the *difference of state* in which essentially the same organized matter appears as two different organisms according to the different conditions in which it may happen to be placed. The sexes, according to the latter view, may be considered as two different aspects of one and the same thing. The male and the female offspring of a given organism both inherit a similar share of materials from both parents, but simply take different courses in the mode of their ontogenetic development.

It is interesting in this connection to recall the beautiful experiment of Maupas[1] on the artificial determination of sexes in a Rotifer, *Hydatina senta*. The Rotifer, as is known, produces three kinds of eggs, viz. two kinds of "summer eggs" and one kind of "winter egg." Of the two kinds of "summer eggs," it is known that the smaller egg always gives rise to the male, and the larger to the female. Under the ordinary circumstance, a certain female *Hydatina* produces exclusively the female eggs, while another female individual produces exclusively the brood of male offspring. Taking advantage of this fact, Maupas tried a series of experiments to determine under what circumstances this exclusive production of the male and the female offspring comes into play. Maupas holds, and his view seems to be amply justified by the results of his experiments, that the ova of the Rotifer up to a certain stage of their ovarian existence are devoid of sex or are neutral. Once this stage is passed, they are fated to develop either into the male or the female organism, as the case may be. Maupas considers that the determining influence which deflects the type of development of the organism, either to the male or to the female side, is due to temperature. If the ovarian ova which maintain the neutral stage as regards their sex are exposed to the influence of a higher temperature, they give rise to a far greater proportion of male organisms; while, on the contrary, if they are exposed to a lower temperature, a far greater proportion of the offspring are females.

In his first experiment, Maupas took five young females of *Hydatina*, and kept them in his laboratory, where the tempera-

[1] Maupas, *Sur la déterminisme de la sexualité chez l'Hydatina senta*, Compt. Rend. Acad. Sci., Paris, T. cxiii, 1891.

ture was maintained between 26° C. and 28° C. The five females were kept till death, and in their lifetime they laid 104 eggs, of which 97 per cent. were males and only 3 per cent. were females. He took another set of five young females, and kept them in a refrigerator where the temperature was between 14° C. and 15° C. They laid 260 eggs during their lifetime, of which 95 per cent. were females and only 5 per cent. were males.

In his second experiment, he took five young females, and kept them in the temperature between 14° C. and 15° C. They laid 110 eggs, of which 76 per cent. gave rise to females and 24 per cent. to males. He then transferred the same five females into the humid chamber, with the temperature 26°–28° C. They produced, up to the time of their death, 118 eggs, of which 81 per cent. gave rise to males and 19 per cent. to females.

In his third experiment, Maupas took six young females, and these when kept in the lower temperature (14°–15° C.) laid 34 eggs, of which 88 per cent. were females and 12 per cent. were males. When the same female parents were placed under the influence of the higher temperature (26°–28° C.), they laid 44 eggs, of which 95 per cent. were males and 5 per cent. were females. Maupas exposed the same females alternately to the higher and the lower temperature, and in one instance fully 100 per cent. of the eggs produced in the higher temperature turned out to be males. In the last four days of their existence they were placed in the cold chamber again, when they produced 50 eggs, of which 83 per cent. were females and 17 per cent. were males.

In short, when the young females of *Hydatina* were placed under the influence of the lower temperature, only 5–24 per cent. of eggs laid gave rise to males, while 76–95 per cent. of the eggs gave rise to females; when, however, they were placed under the influence of the higher temperature, 81–100 per cent. of the eggs were males and 0–19 per cent. were females.

These observations of Maupas are most conclusive in showing that external influence does actually determine the sex of the offspring. The works of Mrs. Mary Treat,[1] on *Lepidoptera*,

[1] Mrs. Mary Treat, *Controlling Sex in Butterflies*, American Naturalist, Vol. 7, 1873.

of Born[1] and of Yung[2] on *Amphibians*, as to the influence of nutrition in the determination of sexes, are well known to all naturalists.

The works of botanists in a similar line of observation are highly instructive, but I cannot dwell on these topics at present. The object of the present paper being only to bring out a certain illustration of general significance in connection with our subject, an extensive multiplication of analogous instances is not exactly to the point.

From what has been said, it is clear that the differentiation of sex in the developing embryo is purely an ontogenetic phenomenon. Observing farther that the conditions of the surroundings can effect such a determining influence as has been described, we may say from one standpoint that the sex-differentiation of the embryo is in the hands of external forces. On the other side, the maleness or the femaleness of the organism may be said to be the result of the responsive reaction on the part of the given protoplasm to the external stimuli. The sex-differentiation is, according to this view, due partly to a property of the protoplasm as determined by its inherent structure, and partly to the action of definite external influences which act upon the protoplasm from without. In this respect, to anticipate my conclusion, I may say *that the phenomenon of sex-differentiation is one with that of irritability, and is the most pronounced of all the phenomena of protoplasmic irritability, because the stimulus acts at an early stage of ontogeny, and thus at the outset profoundly deflects the course of behavior of the whole organism.*

It seems rather superfluous to dwell, in this place, on the well-established conception of the relation between the stimulus and the protoplasmic reaction. If I touch briefly on this subject, as I venture to do in the following, it is not with the view of unnecessarily repeating what is already fully treated in standard works on the subject, but to illustrate more fully exactly what I mean by identifying the phenomenon of sex-

[1] G. Born, *Experimentelle Untersuchungen über die Entstehung der Geschlechtsunterscheide*, Breslauer ärztliche Zeitschrift, 1881.

[2] E. Yung, *De l'influence de la nature des aliments sur la sexualité*, Compt Rend. Acad. Sci., Paris, T. xciii, 1881.

differentiation with that of irritability, and to point out the close parallels which exist between the two.[1]

"When by a touch on a trigger the explosion of a pistol is caused, we do not say that the pistol is irritable, but when in an organism a similar release of stored-up energy occurs, we apply the term irritability to the phenomenon, and we call the influence which produced the change a stimulus."[2] Or, in the words of Sachs, the stimulus is the name which is given to any alteration in the environment of the irritable organs by means of which stimulation is caused, such as intensity of light, variation of temperature, alteration of electrical conditions, instantaneous shocks, sudden pressure, etc. Considered from another point of view, irritability is fundamentally nothing other than the reactions of the organs or organism towards the outside world, in the way determined by the conditions of their inherited structure. Among such specific phenomena of irritability as heliotropism, geotropism, etc., Sachs also includes such phenomena as gall-formation, which is the abnormal reaction of the vegetable protoplasm towards the abnormal stimulus caused by the insect. He also includes in this category the phenomena that follow the fecundation of the ovum, the ovum being an organism which, under the stimulus from without of the fertilizing substance reacts in so astonishing a manner that new processes of configuration and growth arise from it. The association of these two phenomena in the same category, viz. gall-formation, and the development of the embryo following fecundation of the ovum, is extremely suggestive. Darwin[3] has already remarked that every species of gall formed by different insects possesses a specific anatomical structure and textural form "as if the gall were an organism *sui generis*." The comparison between the phenomena of gall-formation and development of the embryo after fecundation of the ovum, becomes still more suggestive when we remember that entirely different kinds of galls are produced on the same plant by different insects, just as different organisms are produced from the ova of the same animal when the ova are fertilized by sperms of different parentage,

[1] I take the following accounts on irritability mostly from Sachs, *Lectures on the Physiology of Plants*; and also from Vines, *Physiology of Plants*.

[2] Francis Darwin, *On Growth-curvatures in Plants*, Nature, Vol. 44, 1891.

[3] Darwin, *Animals and Plants under Domestication*, Vol. II.

as is illustrated in the difference observable between a normal offspring of the same species and a hybrid.

A conspicuous feature of the phenomena of irritability, to follow Professor Sachs again, is that they correspond with the stimulus neither qualitatively nor quantitatively, and it is in this very fact that the essential distinction between the phenomena of irritability and simple mechanical and physical and chemical action lies. The explanation of this remarkable circumstance lies in the irritable structure of the organ itself. The clearest expression of the internal condition of an irritable organ may be obtained by saying that its parts are in a condition of unstable equilibrium. Hence any sudden change in the surrounding conditions may serve to upset the equilibrium and precipitate a change, the final outcome of which is that the protoplasm is bound to follow either one direction or the other. As has been already stated, any deviation in the constitution of the protoplasm that takes place at the beginning of the life-history of the organism must extend through the whole series of its cell derivatives, and hence the effects of the changes in the surroundings, which may be difficult to detect in the early stages, become more and more discernible as the growth and development of the organism proceed. The organisms up to a certain stage of their existence are neutral as regards sex, as the result of experiments leads us to infer. At this stage of sexual neutrality, the organism appears to be potentially capable of assuming either the female or the male organization. *Whether* it becomes the male or the female is entirely due to the play of external forces. It is objectionable to call this stage of neutral sexuality a stage of hermaphroditism, as it has been designated by some naturalists, for hermaphroditism implies the existence of two distinct sexual characters, while neutrality implies the existence of a third but distinct stage, in which any character approaching either male or female is presumed to be entirely absent.

The view that the development of two sexes implies the existence of two different conditions of the surroundings, holds true in the development of two sexual cells, even when they are developed in one and the same organism, as in some hermaphroditic mollusca, in which the two sexual cells may arise in one and the same alveolus of the germ-gland. The male cell leads a free and a more or less migratory existence from

a very early stage of its development, while the female cell is sessile and non-migratory up to the last stage of its ovarian existence. The ovum lies close to the wall of the alveolus and is surrounded with the follicular cells, while the sperm-cell drops into the lumen of the alveolus and there completes its metamorphosis. This difference of conditions, in which the male and female sexual cells respectively develop in the same germ-gland, has been already pointed out by Platner[1] in *Arion*, and I have witnessed the same fact in a number of other organisms.

There is still another important feature in which the phenomena of sex-differentiation approximate to those of irritability. The most vital peculiarity of irritable organs, as Sachs says, lies less in the fact that their parts can be set in motion in virtue of the unstable equilibrium than in the fact that they subsequently again resume their irritable condition — their unstable equilibrium.

Exactly the same phenomenon takes place in connection with sexual differentiation. It is important to bear in mind at the outset certain superficial distinctions that exist between the phenomena of irritability as exhibited in the *growing irritable organism* and in the *mature irritable organ* of the adult organism. While the same irritable state of protoplasm returns again and again in an organ after proper restitution of its material, the case is somewhat different in an irritable organism during its growing period, for the simple reason that a greater part of the material which constitutes such an organism has been made irreversible by its growth. As a consequence, the whole mass of the growing organism does not reassume the irritable state in the way that an irritable organ does. But the return of the whole organism to a highly irritable state is attained in quite another way; namely, by the formation of a unicellular embryo, such as the fertilized ovum in the sexual, and the parthenogenetic ovum in the non-sexual organism.

To return to the consideration of irritability in the matured organ and in the developing organism, we may observe that all of the material which the organism inherits from the par-

[1] Platner, *Zur Bildung der Geschlechtsprodukte bei den Pulmonaten*, Arch. *f.* Mikr. Anat., Bd. xxvi, 1886.

ents is not entirely consumed for the building up of the individual animal. A small portion of it goes to the formation of the germ-cell, which later develops into the sperm-cell or the egg-cell, as the case may be. Thus the parts of an individual organism become divided into two fundamentally different structures which have been called by Weismann the "*soma*" and the "*germ.*" Galton[1] designated these two parts of the organism as the "*patent*" and the "*latent*" part respectively; Jäger,[2] as the "*ontogenetic part*" and the "*phylogenetic part*"; and Rauber,[3] as the "*personal part*" and the "*germinal part.*"

There are several other eminent naturalists who have given expression to a similar view on this subject, but it is entirely unnecessary to enter into any historical review of the question at present. The point which is most important to us is the bearing of such a view of animal organization upon the question we have been considering. If the phenomena of sex-differentiation of the organism were to be identified with that of the irritability of an organ which regains its original irritable state after a short interval of restitution, it is evident that the period covered by the life-history of the individual organism of both sexes must be considered as one long continuous series of the reactions of the protoplasm to the surroundings. The return of the whole organism to its original irritable stage, as has already been stated, is accomplished by the formation of the unicellular embryo or by the union of two sexual cells which were reserved in the "germinal part" of the male and female organism. The period, then, covered by the manifestation of irritable phenomena in a matured organ is comparable to the whole life-history of the growing organism; and the recurrence of the irritable condition in the organ corresponds to the production of the unicellular embryo, which is ready to repeat in turn a series of developmental phenomena similar to those which its parents had already undergone before it. There is really no fundamental difference between the irritability of the growing organism and that of the organ.

[1] Galton, *On Blood Relationship*, Proc. Roy. Soc., XX, 1872.

[2] Jäger, *Physiologische Briefe über Vererbung*, reprinted in his Lehrbuch der allgem. Zoologie, II, 1878.

[3] Rauber, *Personaltheil und Germinaltheil des Individuums*, Zool. Anz. IX. In this paper Rauber gives references to his earlier writings on the subject.

The point which requires our special consideration is that condition of the surroundings which determines the direction along which the non-sexual embryo develops. Maupas' experiments have shown conclusively that the variation of temperature exercises a controlling influence upon the type of the development of the non-sexual organism; while the researches of Born and Yung tend to show that the condition of nutrition has a similar controlling influence. It is probable that several other agencies may be able to bring about the same results in the differentiation of sex as that produced by variation in nutrition and temperature. For it seems probable, from what has been said, that the influence of these two factors cannot be considered in any other light than that of a stimulus, and the forces which act as such a stimulus may not be restricted to the two already mentioned. It is not easy to ascertain, however, the exact potentiality of constitution whereby one and the same organism which develops into a female under certain circumstances, is at the same time capable of developing into a male organism when placed in different surroundings. This is, nevertheless, a fact, and it does not seem unreasonable, therefore, to consider that that structure or quality which appears in the male organism as distinctly masculine, *becomes* in the organism of opposite sex the very attribute of what we consider as distinctively feminine. According to this view, then, the two different qualities which characterize the two organisms of opposite sexes may be considered simply as two different phases of one and the same substance, which are brought about under the influence of different surroundings.

Before concluding this paper there are a few points which call for special remark: —

(1) It is obvious, according to the present view, that because two masses of the same kind of protoplasm react in two different ways towards two different stimuli, each develops respectively into a male and a female organism, and because they develop into two different organisms, each assumes the particular characteristics peculiar to each sex. This constitutional peculiarity of two sexes extends down to the sexual cells. The sexual differentiation of the organism does not exist, properly speaking, for the purpose of bringing together the two germ-cells, as is frequently assumed by some naturalists, but

the union of two sexual cells is itself the inevitable consequence of the sexual differentiation of the organism at the outset. Thus, instead of the necessity of the union of the germ-cells being the cause of the sexual differentiation of the organism, the sexual differentiation of the organism is the cause of the union of the germ-cells.

(2) The present view differs, moreover, from that in which the differences of sex are considered due to those differences existing between the anastate and katastate of the protoplasm. Instead of recognizing predominant katabolism as the male characteristic and predominant anabolism as the female characteristic, maleness and femaleness are considered to be due to two different kinds of katabolism or irritability of the protoplasm. For irritability of protoplasm is nothing more than the internal explosion of its higher complex substance into simpler and more stable substances, and this process of explosive change is what we understand as destructive metabolism or katabolism. According to the present view, it is the nature of the direction along which the katabolic changes of the protoplasm take place, and not the difference exemplified in the alternating phases of the protoplasmic changes, as anabolism and katabolism, that lies at the bottom of the phenomena of sex-differentiation.

(3) The remarkable phenomenon of the "action at a distance" between the two sexual cells observed by several naturalists, which Hæckel[1] has recently ascribed to the existence of what he calls "*erotischer Chemotropismus*," must be considered as the repetition of the same phenomenon of irritability. In this case, it may be considered that each sexual cell acts as a stimulus to the other, owing to the difference of constitution which they temporarily assume. By the time the close approximation of their essential sexual substance is accomplished, the difference between the sperm-nucleus and the egg-nucleus completely disappears, and one morphological element — the segmentation nucleus — which cannot be called either male or female is the result. Maupas' conclusion[2] that "*La fécondation, en dernière analyse, est un phénomène distinct et indépendent de la sexualité*," is highly instructive in this connection, if we

[1] Hæckel, *Anthropogenie*, 4th edition, 1891, Leipzig.

[2] Maupas, *Le rejeunissement karyogamique chez les Ciliés*, Arch. de zool. exp. et gén, T. VII, 1889, p. 479.

define fecundation as *a more or less complete approximation of two pronuclei, just so soon as they can be considered a single morphological element in the ovum.*

The facts which seemed to support this view I have already presented elsewhere.[1] I have since determined, in the newt (*Diemyctylus viridescens*, Raf.), through the kindness of my friend, Dr. Edwin O. Jordan, that the two sexual cells which react differently in an unmistakable manner, to the micro-chemical test during the whole stage of their maturation, and during the early stages of fecundation, become more and more alike toward the completion of the latter process, and at the time when the two pronuclei come closely into contact, the micro-chemical reactions of the "male" and the "female" pronuclei become identical. Similar results were obtained by Lukjanow, as has already been mentioned, in the *Ascaris* of the dog. Lukjanow killed the ovum with corrosive sublimate, and applied the differential method of staining to the pronuclei. Lukjanow's staining substance consisted of hæmatoxylin, safranin, and aurantia. The micro-chemical reactions of the two pronuclei, according to this method, are "almost completely alike," although there exist some slight differences as in the number of vacuoles in the nucleolus and in other minor points. My study on the same subject leads essentially to the same result as that of Lukjanow, although pursued with different methods and on a different animal. The difference which exists between the two pronuclei is simply the difference which distinguishes one individual from another of the same species, as was pointed out by Weismann.

(4) I have already mentioned elsewhere that the sperm-cell undergoes a much more varied series of changes of form and of color-reaction during the period of its maturation than does the ovum in the corresponding period. Thus the law of the greater complexity of the male type of development as compared with that of the female type in "secondary sexual characters," as recognized by Hunter and Darwin, extends even to the essential parts of the "primary sexual character." In short, the phenomena of sex-differentiation extend through the whole organization, including both the "germinal" and the "personal"

[1] *On the Significance of Spermatogenesis* (Abstract), Amer. Nat., July, 1892.

parts of the organism. The organism is either a male or a female, not by the difference of "primary sexual characters" alone, but by the difference which saturates the whole of its entire structure. Such a difference is, however, neither absolute nor permanent. It is a temporary differentiation of protoplasm into one of two different directions, and sooner or later comes back to the original neutral or non-sexual state from which it started, thus manifesting the phenomenon characteristic of all protoplasmic irritability.

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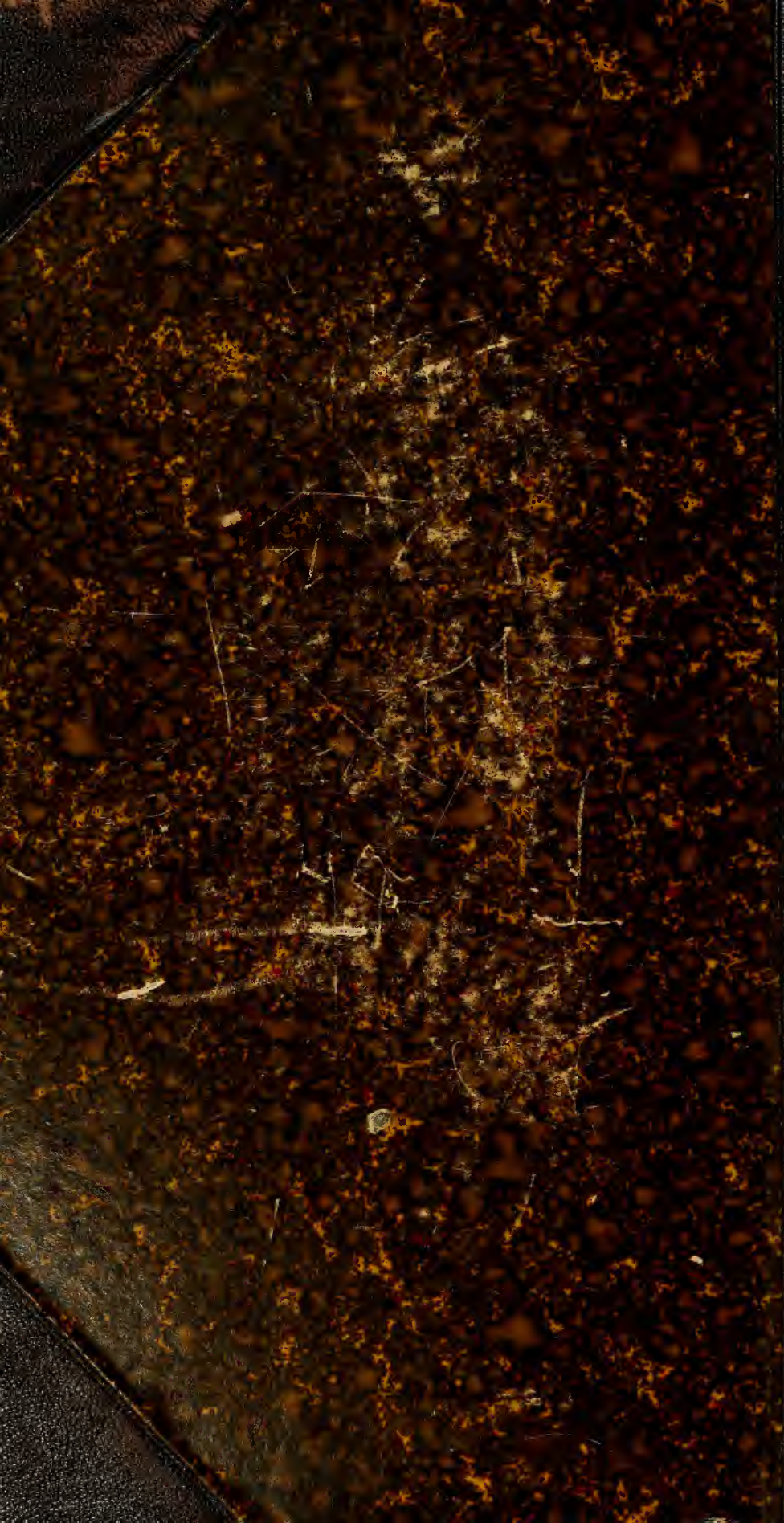
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